



National Library
of Canada

Bibliothèque nationale
du Canada

Canadian Theses Service

Service des thèses canadiennes

Ottawa, Canada
K1A 0N4

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, tests publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30.

THE UNIVERSITY OF ALBERTA

ANALYSIS OF DIFFERENTIAL EQUATION MODELS
OF MUTUALISM WITH A FOOD CHAIN

by

(C)

Ravinder Kumar

A THESIS SUBMITTED TO

THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

Applied Mathematics

DEPARTMENT OF MATHEMATICS

EDMONTON, ALBERTA

FALL, 1988

Permission has been granted to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film.

The author (copyright owner) has reserved other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without his/her written permission.

L'autorisation a été accordée à la Bibliothèque nationale du Canada de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur (titulaire du droit d'auteur) se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation écrite.

ISBN 0-315-45745-7

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: Ravinder Kumar

TITLE OF THESIS: ANALYSIS OF DIFFERENTIAL EQUATION MODELS OF MUTUAL-
ISM WITH A FOOD CHAIN

DEGREE FOR WHICH THESIS WAS PRESENTED: Doctor of Philosophy

YEAR THIS DEGREE GRANTED 1988

Permission is hereby granted to THE UNIVERSITY OF ALBERTA LIBRARY to reproduce single copies of the thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

Ravinder Kumar
SIGNED

PERMANENT ADDRESS:

Dept. of Mathematics
University of Alberta
Edmonton, Alberta T6G 2G1

Date Sept 10, 88

THE UNIVERSITY OF ALBERTA
THE FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Analysis of Differential Equation Models of Mutualism with a Food Chain submitted by Ravinder Kumar in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Applied Mathematics

H. d. Freedman

Supervisor

Jack W. Marshall

Barry G. Bennett

J. E. Lewis
Bryan P. Wood

R. P. Hodder

External Examiner Date

To Mom, Dad, Rajendra and Surrender

ABSTRACT

In recent years there has been increased interest in mathematical models involving mutualism. In this thesis we consider deterministic models of a mutualist's interaction with a food chain. We derive criteria for the existence and non-existence of the various equilibria of our models. Also criteria for the existence of periodic solutions are developed. For a four-dimensional ordinary differential equation model, a criterion for the global asymptotic stability of the interior equilibrium is developed. Also the question of uniform persistence versus extinction is considered for the various mutualistic interactions of the mutualist with the food chain. Criteria for situations under which the model exhibits reversal of outcome are derived. Results are interpreted biologically and several examples are given.

ACKNOWLEDGEMENTS

I wish to express my deep gratitude to my supervisor, Professor H.I. Freedman, for his interest, expert advice and encouragement throughout the preparation of this thesis. I am also grateful to him for providing me an opportunity to work in Mathematical Biology.

I would also like to thank Professor John F. Addicott and Professor Joseph W.-H. So for their advice during the course of this work.

I am grateful to Professor L.H. Erbe for his encouragement and advice over the years.

Financial support received from the Department of Mathematics is gratefully acknowledged.

I would also like to express my thankfulness to my family and friends for their encouragement and advice.

Finally, I wish to thank Mrs. Christine Fischer for her skillful typing and for her cooperation.

TABLE OF CONTENTS

Chapter	Page
1 INTRODUCTION	1
2 MATHEMATICAL PRELIMINARIES	5
2.1 Autonomous Systems	5
2.2 A Comparison Theorem	11
2.3 On the Roots of a Polynomial	12
2.4 Dynamical Systems	13
3 MUTUALIST-FOOD CHAIN MODEL	20
3.1 The Model	20
3.2 Facultative Mutualism with the Prey	22
3.3 Facultative Mutualism with the Second Trophic Level	26
3.4 Obligate Mutualism with the Second Trophic Level	27
3.5 Obligate Mutualism with the Top-Predator	28
4 EXISTENCE, NON-EXISTENCE AND STABILITY OF EQUILIBRIA	30
4.1 Criteria for the Existence and Non-Existence of Equilibria	30
4.2 Stability of Equilibria	34
5 GLOBAL STABILITY AND PERIODIC SOLUTIONS	45

5.1 Global Asymptotic Stability	45
5.2 Periodic Solutions	55
6 FACULTATIVE MUTUALISM WITH THE PREY	60
6.1 Preliminaries	60
6.2 Uniform Persistence	61
6.3 Extinction	72
6.4 Reversal of Outcome	75
7 MUTUALISM WITH HIGHER-TROPHIC LEVELS	81
7.1 Preliminaries	81
7.2 Uniform Persistence	81
7.3 Extinction	99
7.4 Reversal of Outcome	102
8 A TIME DELAY MODEL	111
8.1 Preliminaries	111
8.2 The Characteristic Equation	112
8.3 Stability and Hopf bifurcation	114
Bibliography	120

CHAPTER 1

INTRODUCTION

This thesis is concerned with mathematical models of mutualism with a food chain, and the behaviour of their solutions. In particular we consider the effect of a mutualist on a food chain. Mutualism is an interaction among different species in which each species benefits the other. It is called facultative mutualism if the species involved can survive in the absence of the interaction. When the interaction is essential for the survival of the species involved the mutualism is termed obligate. In the degenerate case when only one species derives benefit while the interaction has no effect on the other the relationship is known as commensalism.

Besides the above mentioned types of mutualism, diverse patterns of mutualistic systems exist. For this reason a single model cannot be expected to describe the interactions of all the systems involving mutualism (Addicott 1984, Wolin 1985). For a long time mutualistic interactions were largely ignored and the dynamics of such systems was poorly understood (Freedman 1980, Boucher 1985). The models discussed involved only two species interactions. However in recent years interest in mutualistic systems has grown considerably.

The Kolmogorov-type model was first used by Rescigno and Richardson (1967) for studying two species facultative mutualism. They derived conditions for an interior equilibrium to be asymptotically stable. Albrecht et al. (1974) showed that the interior equilibrium is globally asymptotically stable with respect

to solutions initiating with positive initial conditions. Freedman et al. (1983) modified the hypotheses for the model to include the Lotka-Volterra model as a special case. They also considered the case of obligate mutualism and showed that for a realistic model there must exist two interior equilibrium points. Addicott and Freedman (1984) have analyzed predator-prey and competition models as modified by the action of a slow growing mutualist. In Haderler and Glas (1983), Hirsch (1982, 1985) and Smith (1986a, 1986b, 1986c) the dynamics of cooperating (i.e. mutualistic) species is considered. For cases where not all the populations are mutualistic, Takeuchi et al. (1978, 1980), and Smith (1986d) have obtained results for competing subcommunities of the mutualists. For mutualist-predator-prey systems Rai et al. (1983), and Freedman et al. (1987 a,b) have analyzed the cases of both facultative and obligate mutualism. Specifically they have obtained criteria for global stability, existence of periodic solutions and uniform persistence.

In Freedman and Rai (1987 c,d) predator-prey-competitor-mutualist and competitor-competitor-mutualist systems have been studied. Rai and Rai (1988) have established boundedness of solutions and derived a criterion for the local stability of the interior equilibrium and extinction of the top-predator in the case of facultative mutualism with the second trophic level, in a simple food chain.

We shall consider a four dimensional deterministic model representing the interactions of a mutualist with a food chain. We now illustrate the existence of such systems with some examples from nature. Monteith (1960), in a study

conducted in Western Ontario, found that the parasitism of sawfly larvae by the parasitoid B. harveyi on the host plant Larix laricina is much lower in the presence of associated plants, which mask the odour of the sawfly larvae and their food plant. Thus here the sawfly larvae benefit from the associated plants, resulting in a commensal relationship.

Wolcott (1942) notes that the successful introduction into Puerto Rico from Brazil of a large wasp, which is parasitic in its larval stage on a mole cricket, apparently depended on the presence in Puerto Rico of two weeds, the flowers of which are the only suppliers of nectar to the wasps. Where these weeds were continuously present in abundance in Puerto Rico, the wasp became established, but where they were scarce or absent even though mole cricket larvae were present in abundance the wasps failed to survive, suggesting that the wasps obligately depend on the weeds for the nectar. Another example arising in agro-ecosystem is described in Nickerson et al. (1977).

In Chapter 2 we introduce some definitions and important results which are used in the analysis of the model in subsequent chapters. In Chapter 3 we describe the model and give hypotheses for facultative and obligate mutualism with different trophic levels of the food chain. In each case we obtain an estimate for the region of attraction. In Chapter 4 we derive criteria for the existence and non-existence of the various equilibria of our model and discuss their local stability. In Chapter 5 we consider the question of global stability for the equilibria of three dimensional submodels and for the interior equilibrium of the system. We

also derive conditions under which Hopf-Bifurcation can occur. In Chapter 6 we study the case of facultative mutualism with the prey. Here we derive criteria for uniform persistence and extinction in three dimensional subsystems and for the system itself. We also show that our model can reverse the outcome predicted by one or more of its three dimensional submodels. In Chapter 7 we consider the case of mutualism with second and third trophic levels. In the final chapter we consider the effect of a discrete time-lag due to gestation.

CHAPTER 2

MATHEMATICAL PRELIMINARIES

The purpose of this chapter is to enunciate some definitions and important theorems which will be used in the subsequent chapters.

2.1 Autonomous Systems

In this section we consider some properties of autonomous systems.

An autonomous system of differential equations is given by

$$x' = f(x), \tag{2.1}$$

where $f: R^n \rightarrow R^n$ is a continuous function.

Since for purposes of modeling we want our model to have unique solutions, we assume that the function f at least satisfies the Lipschitz condition, so that the initial value problem corresponding to (2.1) has a unique solution.

Definition 2.1 A point $p \in R^n$ is called an equilibrium point of (2.1) if $f(p) = 0$.

An important property of autonomous systems is the fact that if $x = x(t)$ is a solution then $x = x(t + t_1)$ is also a solution for any constant t_1 .

Consider a solution $x = x(t)$ with $x(0) = x_0$. If this solution exists for all $t \geq 0$ then we call the set $O^+(x) = \{x(t) : t \geq 0\}$ the positive semi-orbit through x_0 . Similarly if the solution exists for all $t \leq 0$, the set $O^-(x) = \{x(t) : t \leq 0\}$ is called the negative-semiorbit through x_0 . Finally if both $O^+(x_0)$ and $O^-(x_0)$ exist then $O(x_0) = \{x(t) : t \in R\}$ is called the orbit through x_0 .

Definition 2.2 If the system (2.1) has a solution $x = x(t)$ defined on a half-line $t \geq t_0$, with $x(t_0) = x_0$ its omega limit set, $\Omega(x_0)$ is the set of points y_0 for which there exists a real sequence $\{t_n\}$, such that $t_n \rightarrow \infty$ as $n \rightarrow \infty$ and $x(t_n) \rightarrow y_0$ as $n \rightarrow \infty$. Similarly, if $x = x(t)$ is defined for $t \leq t_0$, we can define its alpha limit set $\Lambda(x_0)$ corresponding to $t \rightarrow -\infty$. Whenever the solution is defined for $-\infty < t < \infty$, its set of limit points is defined to be $\Omega(x_0) \cup \Lambda(x_0)$.

Definition 2.3 A set M in R^n is called a invariant set of (2.1) if for any x_0 in M the solution of (2.1) through x_0 , belongs to M for $-\infty < t < \infty$. A set M is called positively (negatively) invariant if for each x_0 in M , the solution $x(t)$ through x_0 belongs to M for $t \geq 0$ ($t \leq 0$).

Definition 2.4 A set $M \subset R^n$ is called a minimal set if it is non-empty, closed and invariant, and does not have any proper subset with these properties.

THEOREM 2.1. *The sets $\Omega(x_0)$ and $\Lambda(x_0)$ are closed and invariant. Furthermore, if $O^+(x_0)$, ($O^-(x_0)$) is bounded, then $\Omega(x_0)(\Lambda(x_0))$ is nonempty, compact and connected.*

For two dimensional autonomous systems the Poincaré-Bendixson theorem describes the omega limit set of a bounded solution. The proof can be found in Hale (1969).

THEOREM 2.2. (Poincaré-Bendixson Theorem) For $n = 2$, let $x(t)$ be a bounded solution of system (2.1). Then either its omega limit set

- (i) is an equilibrium point, or
- (ii) is a periodic orbit, or
- (iii) contains one or more equilibrium points together with saddle connections.

The following theorem provides a criterion for proving the non-existence of periodic solutions for a two dimensional system of autonomous differential equations.

THEOREM 2.3. (Dulac Theorem) With $n = 2$ in (2.1), let $f_1(x_1, x_2)$ and $f_2(x_1, x_2)$ be continuously differentiable functions. If there exists a continuously differentiable, positive function $B(x_1, x_2)$ in a simply connected domain D such that $\frac{\partial(Bf_1)}{\partial x_1} + \frac{\partial(Bf_2)}{\partial x_2}$ does not change sign in D and is not identically zero in any open subdomain of D , then the system (2.1) has no periodic solutions in D .

Next we give a criterion for the global asymptotic stability of an equilibrium point of (2.1). The various definitions of stability and basic results for stability of an equilibrium point and that of a periodic solution can be found in the book of Coddington and Levinson (1955).

Let $V(x)$ be a scalar function defined on an open set $G \subseteq R^n$, such that $V(x)$ is bounded below in G . The derivative $\dot{V}$ of V along the solutions of the

system (2.1) is defined as

$$\dot{V}(x) = V'(x) \cdot f(x) = \sum_{i=1}^n \frac{\partial V}{\partial x_i} f_i(x).$$

Whenever $\dot{V} \leq 0$, the function V is called a Lyapunov function on G .

The following result gives a criterion for the global asymptotic stability of an equilibrium point.

THEOREM 2.4. *If $V(x)$ is a Lyapunov function on G and $V(x) \rightarrow \infty$ as $x \rightarrow \partial G$ (and for $\|x\| \rightarrow \infty$, if G is unbounded) then the omega limit set of any solution of the system (2.1) approaches the largest invariant set M of (2.1) in the set $\{x \in G : \dot{V} = 0\}$. In particular, if M is a point x_0 then the solution $x = x_0$ is globally asymptotically stable in G .*

THEOREM 2.5. (C^L -Hopf Bifurcation) Consider the system of differential equations

$$x' = F(x, \mu), \quad x \in R^n, \quad (2.2)$$

where μ is the bifurcation parameter. If

- (i) $F(0, \mu) = 0$ for μ in an open interval containing 0, and $0 \in R^n$ is an isolated equilibrium point of (2.2),
- (ii) all partial derivatives of the components F_i of the vector F of orders $\leq L + 2$ ($L \geq 2$) exist and are continuous in x and μ in a neighborhood of $(0, 0)$ in $R^n \times R^1$,

(iii) $A(\mu) = D_x F(0, \mu)$ has a pair of complex conjugate eigenvalues λ and $\bar{\lambda}$ such that

$$\lambda(\mu) = \alpha(\mu) + i\omega(\mu),$$

where

$$\omega(0) = \omega_0 > 0, \alpha(0) = 0, \alpha'(0) \neq 0,$$

(iv) the remaining $n - 2$ eigenvalues of $A(0)$ have strictly negative real parts, then the system (2.2) has a family of periodic solutions: there exist an $\epsilon_p > 0$ and a C^{L+1} -function $\mu^p(\epsilon)$,

$$\mu^p(\epsilon) = \sum_1^{[\frac{L}{2}]} \mu_{2i}^p \epsilon^{2i} + O(\epsilon^{L+1}) \quad (0 < \epsilon < \epsilon_p)$$

such that for each $\epsilon \in (0, \epsilon_p)$ there exists a periodic solution $p_\epsilon(t)$, occurring for $\mu = \mu^p(\epsilon)$. There is a neighbourhood η of $x = 0$ and an open interval I containing 0 such that for any $\mu \in I$ the only nonconstant periodic solutions of (2.2) that lie on η are members of the family $p_\epsilon(t)$ for values of ϵ satisfying $\mu^p(\epsilon) = \mu$, $\epsilon \in (0, \epsilon_p)$. The period $T^p(\epsilon)$ of $p_\epsilon(t)$ is a C^{L+1} -function

$$T^p(\epsilon) = \frac{2\pi}{\omega_0} \left[1 + \sum_1^{[\frac{L}{2}]} \tau_{2j}^p \epsilon^{2j} \right] + O(\epsilon^{L+1}), \quad (0 < \epsilon < \epsilon_p).$$

Exactly two of the Floquet exponents of $p_\epsilon(t)$ approach 0 as $\epsilon \downarrow 0$. One is 0 for $\epsilon \in (0, \epsilon_p)$, and the other is a C^{L+1} function

$$\beta^p(\epsilon) = \sum_1^{[\frac{L}{2}]} \beta_{2i}^p \epsilon^{2i} + O(\epsilon^{L+1}) \quad (0 < \epsilon < \epsilon_p).$$

The periodic solution $p_\epsilon(t)$ is orbitally asymptotically stable with asymptotic phase if $\beta^p(\epsilon) < 0$ but is unstable if $\beta^p(\epsilon) > 0$. If there exists a first nonvanishing coefficient μ_{2k}^p ($1 \leq k \leq [\frac{L}{2}]$), then there is an $\epsilon_1 \in (0, \epsilon_p]$ such that the open interval

$$I_1 = \{\mu | 0 < \mu / \mu_{2k}^p < \mu^p(\epsilon_1) / \mu_{2k}^p\}$$

has the following properties. For any μ in I_1 there is a unique $\epsilon \in (0, \epsilon_1)$ for which $\mu_{\epsilon}^p = \mu$. Hence the family of periodic solutions $p_\epsilon(t)$ ($0 < \epsilon < \epsilon_1$) may be parameterized as $p(t, \mu)$ ($\mu \in I_1$). For $\mu \in I_1$, the period $T(\mu)$ and Floquet exponent $\beta(\mu)$ are C^L -functions of $|\mu|^{1/k}$. The first nonvanishing coefficient β_{2k}^p is given by

$$\beta_{2k}^p = -2\alpha'(0)\mu_{2k}^p$$

and

$$\text{sgn}\beta(\mu) = \text{sgn}\beta_{2k}^p \quad (\mu \in I_1).$$

Thus the members $p(t; \mu)$ ($\mu \in I_1$) of the family of periodic solutions are orbitally asymptotically stable with asymptotic phase if $\beta_{2k}^p < 0$ and are unstable if $\beta_{2k}^p > 0$.

The proof of the above theorem can be found in Hassard et al. (1981).

The next two definitions will be used extensively in the following chapters.

Definition 2.5 Given n real variables $x_1, x_2, \dots, x_n$ we denote the positive orthant in R^n by $R_{x_1 \dots x_n}^+$ and its closure by $\bar{R}_{x_1 \dots x_n}^+$. Furthermore, any m -dimensional subsystem of (2.1) obtained by setting $n - m$ variables, say, x_{j+1} to x_{n-m+j} identically equal to zero in (2.1) will be referred to as a subsystem in $R_{x_1 \dots x_j x_{n-m+j+1} \dots x_n}^+$, whenever all the components of its initial value vector are positive.

Definition 2.6 A subsystem in $R_{x_1 \dots x_j x_k \dots x_n}^+$ is said to exhibit extinction with respect to $\{x_{\ell_1}, \dots, x_{\ell_p}\}$, denoted $\mathcal{E}_{x_{\ell_1} \dots x_{\ell_p} \rightarrow 0}$ in $R_{x_1 \dots x_j x_k \dots x_n}^+$ if there exists $\{\ell_i\}_1^p$ ($1 \leq \ell_i \leq j$ or $k \leq \ell_i \leq n$) such that for every solution starting in $R_{x_1 \dots x_j x_k \dots x_n}^+$, we have

$$\lim_{t \rightarrow \infty} x_{\ell_i} = 0 \quad (1 \leq i \leq p).$$

2.2 A Comparison Theorem

In this section we give a comparison theorem which will be employed in Chapter 3 to obtain an estimate for the region of attraction for our model.

THEOREM 2.6. Let $U(t, u)$ and $V(t, u)$ be continuous functions on an open (t, u) -set $E \subset R \times R$ and satisfy

$$V(t, u) \leq U(t, u).$$

Let $u = u^0(t)$ be the maximal solution of

$$u' = U(t, u(t)), \quad u(t_0) = u_0$$

and $v = v(t)$ be a solution of

$$v' = V(t, v), \quad v(t_0) = v_0 \quad (\leq u_0)$$

on an interval $[t_0, t_0 + a]$. Then on any common interval of existence of $u^0(t)$ and $v(t)$,

$$v(t) \leq u^0(t).$$

The proof can be found in Hartman (1982).

2.3 On the roots of a Polynomial

We shall need the Routh-Hurwitz criterion for obtaining necessary and sufficient conditions for the asymptotic stability of the equilibria of our system. The Orlando formula will prove useful for obtaining a criterion for the existence of periodic solutions for our model. Below we give the statements for both of these results. Their proofs can be found in Gantmacher (1959).

Routh-Hurwitz Criterion All the roots of the real polynomial

$$f(\lambda) = a_0 \lambda^n + a_1 \lambda^{n-1} + \dots + a_n \quad (a_0 > 0) \quad (2.3)$$

have negative real parts if and only if the Hurwitz determinants Δ_i , $1 \leq i \leq n$ are positive, where

$$\Delta_1 = |a_1|, \Delta_2 = \begin{vmatrix} a_1 & a_3 \\ a_0 & a_2 \end{vmatrix}, \quad \Delta_3 = \begin{vmatrix} a_1 & a_3 & a_5 \\ a_0 & a_2 & a_4 \\ 0 & a_1 & a_3 \end{vmatrix},$$

$$\Delta_n = \begin{vmatrix} a_1 & a_3 & a_5 \dots & 0 \\ a_0 & a_2 & a_4 \dots & 0 \\ 0 & a_1 & a_3 \dots & 0 \\ 0 & a_0 & a_2 \dots & 0 \\ \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & a_n \end{vmatrix}.$$

The Orlando Formula

Let $\lambda_1, \lambda_2, \dots, \lambda_n$ be the roots of the polynomial (2.3). Then the $(n-1)$ st Hurwitz determinant satisfies

$$\Delta_{n-1} = (-1)^{\frac{n(n-1)}{2}} a_0^{n-1} \prod_{i < k}^{1, \dots, n} (\lambda_i + \lambda_k). \quad (2.4)$$

2.4 Dynamical Systems

Here we give some results on the dynamical systems which will be used to obtain criteria for uniform persistence.

Let $\mathcal{E}$ be a locally compact metric space with metric d . For any subset S of $\mathcal{E}$ we shall use $\overset{\circ}{S}$, ∂S , $\bar{S}$ to denote its interior, boundary and closure, respectively. Given a closed subset E of $\mathcal{E}$, we consider a continuous flow $\mathcal{F} = (E, R, \pi)$ on E , where R is set of real numbers and $\pi(x, t)$ is a continuous map from $E \times R$ to E such that $\pi(\pi(x, t), s) = \pi(x, t + s)$ for all $x \in E$, $s, t \in R$.

We shall assume that ∂E is invariant under $\mathcal{F}$, i.e., $\pi(\partial E \times R) \subset \partial E$. We denote the restriction of $\mathcal{F}$ to ∂E by $\partial \mathcal{F}$.

Definition 2.7. For $x \in E$ the mapping π induces a continuous map $\pi_x : R \rightarrow E$, determined by $\pi_x(t) = \pi(x, t)$, which is called a motion through x .

Definition 2.8 Given a set $M \subset E$ its stable set $W^s(M)$ is defined to be

$$W^s(M) = \{x \in E : \Omega(x) \neq \emptyset, \Omega(x) \subset M\}.$$

Similarly, the unstable set $W^u(M)$ is defined as

$$W^u(M) = \{x \in E : \Lambda(x) \neq \emptyset, \Lambda(x) \subset M\}.$$

Definition 2.9 The weakly stable set $W_w^s(M)$ of a set $M \subset E$ is defined to be $\{x \in E : \Omega(x) \cap M \neq \emptyset\}$ and the weakly unstable set $W_w^u(M)$ is defined to be $\{x \in E : \Lambda(x) \cap M \neq \emptyset\}$.

Definition 2.10 Given a non-empty set M of $\mathcal{E}$ and $\delta > 0$ we define

$$S(M, \delta) = \{x \in \mathcal{E} : d(x, M) < \delta\}.$$

In the following we assume that $M \subset E$ is a compact set.

Definition 2.11 If there exists a $\delta > 0$ such that $S(M, \delta) \subset W^s(M)$, then M is called an attractor. The minimal set M such that $W^s(M) = E$, is called the region of attraction. If $\exists \delta > 0$ such that $S(M, \delta) \subset W^u(M)$, then M is called a negative attractor.

Definition 2.12 If for all $\epsilon > 0$ there exists a $\delta(\epsilon) > 0$, such that $O^+(S(M, \delta)) \subset S(M, \epsilon)$, M is called stable. Further if M is both stable and an attractor it is called asymptotically stable.

Definition 2.13 Let M be a negative attractor. If there exists an $\eta > 0$ such that $x \in S(M, \eta)/M$ implies that $\Omega(x) \cap M = \emptyset$, M will be said to be completely unstable.

Definition 2.14 A motion π_x is said to be positively (Lyapunov) stable in a subset N of E , if for any $\epsilon > 0$, there is a $\delta > 0$ such that $y \in N \cap S(x, \delta)$ implies

$$d(x(t), y(t)) < \epsilon \text{ for } t \geq 0. \quad (2.5)$$

If inequality (2.5) holds for $t \leq 0$ or $-t \in R$ then the motion π_x is called negatively stable or stable in both directions.

Definition 2.15 If $A \subset B \subset E$, then the motions through A (i.e. motions π_x with $x \in A$) will be called uniformly positively stable, uniformly negatively stable, or uniformly stable in both directions in B , if given any $\epsilon > 0$, there is a $\delta > 0$ such that $d(x(t), y(t)) < \epsilon$ for $t \geq 0$, $t \leq 0$ or $-\infty < t < \infty$ respectively when $x \in A$, $y \in B$ and $d(x, y) < \delta$.

Definition 2.16 A set D of real numbers is called relatively dense if there is a $T > 0$ such that

$$D \cap (t - T, t + T) \neq \emptyset \text{ for all } t \in R.$$

Definition 2.17 A motion π_x is said to be almost periodic if for every $\epsilon > 0$ there exists a relatively dense subset of numbers $\{\tau_n\}$ called displacements such that

$$d(x(t), x(t + \tau_n)) < \epsilon,$$

for all $t \in R$ and each τ_n .

THEOREM 2.7. Let $f(t)$ be a real or complex valued almost periodic function on R . Then the mean value

$$M[f] = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^{t+T} f(u) du$$

exists and is independent of t .

The proof can be found in Hale (1969).

THEOREM 2.8. Let the motion π_x be almost periodic and let $\bar{O}(x)$ be compact.

Then

- (i) $\bar{O}(x)$ is a compact minimal set,
- (ii) every motion π_y with $y \in \bar{O}(x)$ is almost periodic,
- (iii) every motion through $\bar{O}(x)$ is uniformly stable in both directions in $\bar{O}(x)$.

The proof can be found in Bhatia and Szegő (1967).

Definition 2.18 The flow $\mathcal{F}$ is called dissipative if for each $x \in E$, $\Omega(x) \neq \emptyset$ and the invariant set $\Omega(\mathcal{F}) = \bigcup_{x \in E} \Omega(x)$ has compact closure.

Definition 2.19 An isolated invariant set M for the flow $\mathcal{F}$ is a non-empty invariant set which is a maximal invariant set in some neighbourhood of itself.

Definition 2.20 The flow $\partial\mathcal{F}$ is called isolated if there exists a finite covering M of $\Omega(\partial\mathcal{F})$ by pairwise disjoint compact isolated invariant sets $M_1, M_2, \dots, M_k$ for $\partial\mathcal{F}$ such that each M_i is also isolated for $\mathcal{F}$. M is then called an isolated covering.

If M, N are isolated invariant sets for $\mathcal{F}$, not necessarily distinct, we shall say that M is chained to N and write this as $M \rightarrow N$, if there exists $x \notin M \cup N$ such that $x \in W^u(M) \cap W^s(N)$.

A chain of isolated invariant sets is a finite sequence $M_1, M_2, \dots, M_k$ with $M_1 \rightarrow M_2 \rightarrow \dots \rightarrow M_k$ ($M_1 \rightarrow M_1$, if $k = 1$). The chain is called a cycle if $M_k = M_1$.

Definition 2.21 $\partial\mathcal{F}$ is called acyclic if for some isolated covering M of $\Omega(\partial\mathcal{F})$, $M = \bigcup_1^k M_i$, no subset of $\{M_i\}$ forms a cycle.

Definition 2.22 The flow $\mathcal{F}$ is called weakly persistent if for all $x \in \overset{\circ}{E}$, $\lim_{t \rightarrow \infty} d(\pi(x, t), \partial E) > 0$; is called persistent if for all $x \in \overset{\circ}{E}$, we have $\lim_{t \rightarrow \infty} d(\pi(x, t), \partial E) > 0$; is called uniformly persistent if there exists $\epsilon_0 > 0$ such that for all $x \in \overset{\circ}{E}$, $\lim_{t \rightarrow \infty} d(\pi(x, t), \partial E) \geq \epsilon_0$.

LEMMA 2.1. (Butler-McGehee Lemma) Let P be an isolated hyperbolic equilibrium in the omega limit set $\Omega(x)$ of an orbit $\mathcal{O}(x)$. Then either $\Omega(x) = P$ or there exists points Q and R in $\Omega(x)$ with $Q \in W^s(P)$ and $R \in W^u(P)$.

The proof can be found in Freedman and Waltman (1984).

THEOREM 2.9. Let $\mathcal{F}$ be a continuous flow on a locally compact metric space E with metric d and boundary ∂E . Let $\partial\mathcal{F}$ be the restriction of $\mathcal{F}$ to ∂E (assumed invariant under $\mathcal{F}$). Assume that

- (i) $\mathcal{F}$ is dissipative;
- (ii) $\mathcal{F}$ is weakly persistent;
- (iii) $\partial\mathcal{F}$ is isolated;
- (iv) $\partial\mathcal{F}$ is acyclic.

Then $\mathcal{F}$ is uniformly persistent.

COROLLARY 2.1. The flow $\mathcal{F}$ has an equilibrium point in $\overset{\circ}{E}$, provided $\overset{\circ}{E}$ is isomorphic to a Euclidean space.

The proofs can be found in Butler, Freedman and Waltman (1986).

The following theorem generalizes the Butler-McGehee Lemma.

THEOREM 2.10. Let M be a compact isolated invariant set for any continuous flow $\mathcal{F}$ on a locally compact metric space. Then for any $x \in W_w^s(M) \setminus W^s(M)$, it follows that

$$\Omega(x) \cap W^s(M) \setminus M \neq \emptyset, \Omega(x) \cap W^u(M) \setminus M \neq \emptyset.$$

(A similar statement holds for $\Lambda(x)$).

THEOREM 2.11. Let $\mathcal{F}$ be a continuous flow on a locally compact metric space E with invariant boundary. Assume that the flow $\mathcal{F}$ is dissipative and the bound-

ary flow $\partial\mathcal{F}$ is isolated and is acyclic with acyclic covering M . Then $\mathcal{F}$ is uniformly persistent if and only if for each $M_i \in M$, $W^s(M_i) \cap \overset{\circ}{E} = \emptyset$.

The proofs of the above two theorems can be found in Butler and Waltman (1986).

Definition 2.23 An orbit $O(x)$, $x \in E$ is called homoclinic if for some equilibrium point P , $O(x) \subset W^s(P) \cap W^u(P)$.

Remark 2.1 For our model the metric space $\mathcal{E} = R^4$ and $E = \bar{R}_{x_1 x_2 x_3 x_4}^+$, the nonnegative cone in R^4 .

CHAPTER 3

MUTUALIST-FOOD CHAIN MODEL

In this chapter we describe the general model of a mutualist's interactions with a food chain. In §3.2-3.5 we give the mathematical formulation of facultative and obligate relationships between the mutualist and the different trophic levels of the food chain. Also, we establish the existence of a region of attraction in each case, showing that the model is well-behaved.

3.1 The Model

We consider the autonomous system,

$$\begin{aligned}\frac{du}{dt} &= uh(u, x, y, z) \\ \frac{dx}{dt} &= \alpha xg(u, x) - yp_1(u, x) - zp_2(u, x) \\ \frac{dy}{dt} &= y(-s_1(u, y) + c_1(u)p_1(u, x)) - zq(u, y) \\ \frac{dz}{dt} &= z(-s_2(u, z) + c_2(u)p_2(u, x) + c_3(u)q(u, y)),\end{aligned}\tag{3.1}$$

$$u(0) = u_0 \geq 0, x(0) = x_0 \geq 0, y(0) = y_0 \geq 0, z(0) = z_0 \geq 0,$$

as a model of a mutualist-food chain interaction, with continuous birth and death processes. The variable $u(t)$ represents the density of mutualists at time t and $x(t)$, $y(t)$, $z(t)$ denote the prey and predator densities. In absence of the mutualist, i.e., when $u \equiv 0$, (3.1) reduces to a food chain model (see Freedman, 1980).

The function $h(u, x, y, z)$ represents the specific growth rate of the mutualist. We assume that $h(u, x, y, z)$ possesses the following properties (Albrecht et al. 1974; Freedman, 1980; Kolmogorov, 1936; Rai et al. 1983).

$$(H1) \quad h(0, x, y, z) > 0, \quad \frac{\partial h}{\partial u}(u, x, y, z) \leq 0.$$

(H2) there exists a unique function, $L(x, y, z) > 0$ such that

$$h(L(x, y, z), x, y, z) = 0.$$

The first condition implies that, independent of the x, y, z populations, u is capable of growing even when rare. Also, the growth rate is assumed to be density dependent and decreases as the population increases. The second condition implies that $L(x, y, z)$ is the mutualist's carrying capacity and in part specifies in what way the predators and prey become part of the mutualist's environment.

The function $g(u, x)$ is the specific growth rate of the prey x in the absence of any predation. We assume that

$$(G1) \quad g(u, 0) > 0, \quad \frac{\partial g}{\partial x}(u, x) \leq 0.$$

(G2) there exists a unique $K(u) > 0$ such that $g(u, K(u)) = 0$.

The condition (G1) implies that the prey population is capable of surviving in the presence or absence of the mutualist and that the growth rate in the absence of predation is density dependent. The condition (G2) implies that $K(u)$ is the carrying capacity of the prey in the absence of predation.

Next, the functions $p_i(u, x)$, $i = 1, 2$ and $q(u, y)$ denote the predator's functional response to the prey and mutualist's densities. They represent the change in density of prey per predator per unit time, as a function of the prey and mutualist densities. We assume that,

$$(P1) \quad p_i(u, 0) = 0, \quad \frac{\partial p_i}{\partial x}(u, x) > 0, \quad i = 1, 2 \quad q(u, 0) = 0, \quad \frac{\partial q}{\partial y}(u, y) > 0.$$

The above conditions imply that in absence of prey there is no predation. Further, the predator response is assumed to be an increasing function of the prey population.

The functions $s_1(u, y)$ and $s_2(u, z)$ are the specific death rates of the predators y and z , in the absence of predation. We make the standard assumption that the death rate is an increasing function of the population:

$$(S1) \quad \frac{\partial s_1(u, y)}{\partial y} > 0, \quad \frac{\partial s_2(u, z)}{\partial z} > 0.$$

The non-negative functions $c_i(u)$, $i = 1, 2, 3$ are the conversion rates of prey biomass to the predator biomass. Also $\alpha > 0$ is a bifurcation parameter. Finally, we assume that all the functions are smooth enough so that existence and uniqueness of initial value problems hold and any required analysis can be carried out.

3.2 Facultative Mutualism with the Prey

In this section we specify the hypotheses for facultative mutualism between the mutualist u and the prey x . In addition to H(1-2), we assume the following for the specific growth rate $h(u, x, y, z)$ of the mutualist:

$$(H3) \quad \frac{\partial h(u, x, y, z)}{\partial x} > 0, \quad \frac{\partial h(u, x, y, z)}{\partial y} \leq 0, \quad \frac{\partial h(u, x, y, z)}{\partial z} \leq 0.$$

$$(H4) \quad \lim_{x \rightarrow \infty} L(x, 0, 0) = \tilde{L} < \infty.$$

The condition (H3) implies that u derives benefit from the prey population and that there might be a cost to the mutualist due to its interactions with the predators. The condition (H4) implies that the mutualist has a finite carrying capacity.

In the case that $\frac{\partial q(u,x)}{\partial u} > 0$, then even in the absence of predation, u acts as a mutualist with respect to x . If $\frac{\partial q(u,x)}{\partial x} < 0$, then there is a cost to x for associating with u and u can be a mutualist of x only by its effect upon the predator(s). If $\frac{\partial q(u,x)}{\partial u} \equiv 0$, the relationship between u and x without predation is commensal.

Further, we assume

$$(P2) \quad \frac{\partial p_i(u,x)}{\partial u} \leq 0, \quad i = 1, 2.$$

This condition implies that the mutualist can benefit the prey by decreasing the predator's response. The mutualist can also benefit the prey by increasing the death rate of y or by decreasing the rate of conversion from prey biomass to the predator biomass:

$$(S2) \quad \frac{\partial s_1(u,y)}{\partial u} \geq 0, \quad c'_1(u) \leq 0, \quad c'_2(u) \leq 0.$$

Also, in order to have a viable system we must have that,

$$(S3) \quad \text{there exists a } \hat{x} \text{ such that } \frac{s_1(0,0)}{c_1(0)} = p_1(0, \hat{x}), \text{ and } \hat{x} < K(0).$$

Finally, the mutualist can also benefit the prey indirectly, by its affect on the dynamics of the top-predator z , i.e. by affecting its death rate $s_2(u,z)$, the predator response function $q(u,y)$ or the rate of conversion $c_3(u)$ of prey biomass into predator biomass.

Now we show that under the above hypotheses a certain set A contains the region of attraction of (3.1). The proof is based on the ideas developed in Freedman and Waltman (1984) and Freedman and So (1985).

THEOREM 3.1. Whenever the hypotheses $H(1-4)$, $G(1,2)$, $P(1,2)$, $S(1-3)$ hold, the set

$$\mathcal{A} = \{(u, x, y, z) : 0 \leq u \leq \tilde{L}, 0 \leq x \leq \tilde{K}, 0 \leq c_1(0)x + y \leq \tilde{M}, \\ 0 \leq c_2(0)x + \tilde{c}_3 y + z \leq \tilde{N}\}, \quad (3.2)$$

where

$$\tilde{L} = \lim_{z \rightarrow \infty} L(x, 0, 0), \quad \tilde{K} = \max_{0 \leq u \leq \tilde{L}} K(u), \quad \tilde{g} = \max_{0 \leq u \leq \tilde{L}} g(u, 0), \\ \tilde{M} = \frac{c_1(0)\tilde{K}}{s_1(0, 0)}(\alpha\tilde{g} + s_1(0, 0)), \quad \tilde{s}_2 = \min_{0 \leq u \leq \tilde{L}} s_2(u, 0), \quad (3.3) \\ \tilde{c}_3 = \max_{0 \leq u \leq \tilde{L}} c_3(u)$$

and

$$\tilde{N} = \frac{1}{s_2(0, 0)}(c_2(0)\tilde{K}(\tilde{s}_2 + \alpha\tilde{g}) + \tilde{c}_3\tilde{M}(\tilde{s}_2 + c_1(0)p_1(0, \tilde{K}))),$$

is positively invariant and attracts all solutions initiating with nonnegative initial conditions.

PROOF: Let $(u(t), x(t), y(t), z(t))$ be any solution with nonnegative initial condition (u_0, x_0, y_0, z_0) . Since

$$u' = uh(u, x, y, z) \leq uh(u, x, 0, 0),$$

whenever $u(t) \geq \tilde{L}$, we get

$$u' \leq uh(\tilde{L}, x, 0, 0) < 0.$$

From this, it follows that $u(t) \leq \tilde{L}$ for all $t \geq 0$, whenever $u_0 \leq \tilde{L}$. Further, if $u_0 > \tilde{L}$ then $u(t) \leq \tilde{L}$, for large t .

Next, let $g_1(x) = \max_{0 \leq u \leq \tilde{L}} g(x)$. Then all solutions of the initial-value problem,

$$x = xg_1(x), \quad x = x_0 \geq 0,$$

satisfy $\limsup_{t \rightarrow \infty} x(t) \leq \tilde{K}$ (see Freedman, 1980), it follows from a standard comparison Theorem (e.g. see Hartman, 1982) that in case $x_0 \leq \tilde{K}$, $x(t) \leq \tilde{K}$ for all $t \geq 0$, otherwise $x(t)$ is bounded above by $\tilde{K}$ for sufficiently large t .

Now, we consider

$$\begin{aligned} (c_1(0)x + y)' &= \alpha c_1(0)xg(u, x) - c_1(0)yp_1(u, x) - c_1(0)zp_2(u, x) \\ &\quad - ys_1(u, y) + yc_1(u)p_1(u, x) - zq(u, y) \\ &\leq \alpha c_1(0)xg(u, x) - ys_1(u, y) \\ &\leq \alpha c_1(0)xg(u, 0) - ys_1(0, 0) + c_1(0)xs_1(0, 0) - c_1(0)xs_1(0, 0) \\ &\leq c_1(0)\tilde{K}(\alpha\tilde{g} + s_1(0, 0)) - s_1(0, 0)(c_1(0)x + y), \end{aligned}$$

i.e.

$$\begin{aligned} c_1(0)x(t) + y(t) &\leq \frac{c_1(0)\tilde{K}}{s_1(0, 0)}(\alpha\tilde{g} + s_1(0, 0)) \\ &\quad - e^{-st} \left(\frac{c_1(0)\tilde{K}}{s_1(0, 0)}(\alpha\tilde{g} + s_1(0, 0) - (c_1(0)x_0 + y_0)) \right) \\ &= \tilde{M} - e^{-st}(\tilde{M} - (c_1(0)x_0 + y_0)). \end{aligned}$$

Thus if $c_1(0)x_0 + y_0 \leq \tilde{M}$, we get

$$c_1(0)x(t) + y(t) \leq \tilde{M} \text{ for all } t \geq 0.$$

Otherwise there exists $T > 0$ such that

$$c_1(0)x(t) + y(t) \leq \tilde{M} \text{ for } t \geq T.$$

Similar arguments can be given to show that the inequality

$$c_2(0)x(t) + \tilde{c}_3 y(t) + z(t) \leq \tilde{N} \quad (3.4)$$

holds for all $t \geq 0$, whenever $c_2(0)x_0 + \tilde{c}_3 y_0 + z_0 \leq \tilde{N}$. Otherwise (3.4) is true for sufficiently large values of t .

3.3 Facultative Mutualism with the Second Trophic Level

The system (3.1) exhibits facultative mutualism between u and y , under the following hypotheses: In addition to $H(1-2)$, $G(1-2)$, $(P1)$, $S(1,3)$, we assume

$$(H3') \quad \frac{\partial h(u, x, y, z)}{\partial x} \leq 0, \quad \frac{\partial h(u, x, y, z)}{\partial y} > 0, \quad \frac{\partial h(u, x, y, z)}{\partial z} \leq 0.$$

$$(H4') \quad \lim_{y \rightarrow \infty} L(0, y, 0) = \tilde{L} < \infty.$$

$$(G3') \quad \frac{\partial q(u, x)}{\partial u} \geq 0.$$

$$(P2') \quad \frac{\partial p_1(u, x)}{\partial u} \geq 0, \quad \frac{\partial p_2(u, x)}{\partial u} \leq 0, \quad \frac{\partial q(u, y)}{\partial u} \leq 0.$$

$$(S2') \quad \frac{\partial s_1(u, y)}{\partial u} \leq 0, \quad \frac{\partial s_2(u, y)}{\partial u} \geq 0, \quad c'_1(u) \geq 0, \quad c'_2(u) \leq 0, \quad c'_3(u) \leq 0.$$

In this case the following set B contains the region of attraction. The proof is similar to Theorem 3.1.

THEOREM 3.2. *Whenever the hypotheses $H(1, 2, 3', 4')$, $G(1, 2, 3')$, $P(1, 2')$, $S(1, 2', 3)$ hold, the set*

$$B = \{(u, x, y, z) : 0 \leq u \leq \tilde{L}, 0 \leq x \leq \tilde{K}, 0 \leq c_1(\tilde{L})x + y \leq \tilde{M}, \\ 0 \leq c_2(0)x + c_3(0)y + z \leq \tilde{N}\}, \quad (3.5)$$

where

$$\begin{aligned}\tilde{L} &= \lim_{y \rightarrow \infty} L(0, y, 0), \quad \tilde{K} = \max_{0 \leq u \leq \tilde{L}} K(u), \\ \tilde{M} &= \frac{c_1(\tilde{L})\tilde{K}}{s_1(\tilde{L}, 0)} (\alpha g(\tilde{L}, 0) + s_1(\tilde{L}, 0)),\end{aligned}\quad (3.6)$$

and

$$\tilde{N} = \frac{1}{s_2(0, 0)} (c_2(0)\tilde{K}(\alpha g(\tilde{L}, 0) + s_2(0, 0)) + c_3(0)\tilde{M}(c_1(\tilde{L})p_1(\tilde{L}, \tilde{K}) + s_2(0, 0)))$$

is positively invariant and attracts all solutions initiating with nonnegative initial conditions.

3.4 Obligate Mutualism with the Second Trophic Level

In this section we consider the case of obligate mutualism between the mutualist u and the predator y . The system (3.1) will exhibit such a behaviour, when in the absence of the mutualist the food chain collapses and the predator y becomes extinct. Thus, we require that the subsystem:

$$\begin{aligned}\frac{dx}{dt} &= \alpha x g(0, x) - y p_1(0, x) - z p_2(0, x) \\ \frac{dy}{dt} &= y(-s_1(0, y) + c_1(0)p_1(0, x)) - z q(0, y) \\ \frac{dz}{dt} &= z(-s_2(0, z) + c_2(0)p_2(0, x) + c_3(0)q(0, y)),\end{aligned}$$

with $x(0) > 0$, $y(0) > 0$ and $z(0) > 0$, exhibit extinction and $\lim_{t \rightarrow \infty} y(t) = 0$.

This happens when condition (S3) is violated (see Freedman et al. 1987), i.e.,

$$(S3'a) \quad \lim_{x \rightarrow \infty} p_1(0, x) \leq \frac{s_1(0, 0)}{c_1(0)} \quad \text{or}$$

$$(S3'b) \quad p(0, \hat{x}) = \frac{s_1(0, 0)}{c_1(0)} \quad \text{and} \quad \hat{x} \geq K(0).$$

The ways in which u and y can benefit each other remain the same as in section 3.3. In conclusion whenever $H(1,2,3'4')$, $G(1,2,3')$, $P(1,2)$ and $S(1,2',3')$ hold, mutualism occurs between u and y and is obligate for the predator. Further, the set β given by Theorem 3.2 still contains the region of attraction.

3.5 Obligate Mutualism with the Top-predator

The system (3.1) exhibits mutualism between u and z , which is obligate for the top-predator z , whenever in addition to $H(1,2)$, $G(1,2,3')$, $P1$, $S(1,3)$, the following assumptions hold:

$$(H3^*) \quad \frac{\partial h(u,z,y,z)}{\partial z} \leq 0, \quad \frac{\partial h(u,z,y,z)}{\partial y} \leq 0, \quad \frac{\partial h(u,z,y,z)}{\partial x} > 0.$$

$$(H4^*) \quad \lim_{x \rightarrow \infty} L(0,0,z) = \bar{L} < \infty.$$

$$(P2^*) \quad \frac{\partial p_2(u,x)}{\partial u} \geq 0, \quad \frac{\partial q(u,y)}{\partial u} \geq 0.$$

$$(S2^*) \quad \frac{\partial s_2(u,y)}{\partial u} \leq 0, \quad c'_2(u) \geq 0, \quad c'_3(u) \geq 0.$$

The following condition ensures that in the absence of u, z will become extinct.

$$(S4^*a) \quad c_2(0) \lim_{x \rightarrow \infty} p_2(0,x) + c_3(0) \lim_{y \rightarrow \infty} q(0,y) \leq s_2(0,0).$$

or

$$(S4^*b) \quad c_2(0)p_2(0,\underline{x}) + c_3(0)q(0,\underline{y}) = s_2(0,0), \text{ for some } \underline{x} \text{ and } \underline{y}, \text{ where } \underline{x} \geq K(0).$$

Finally the mutualist can indirectly benefit the predator z , by affecting the death rate, the predator response function or the conversion rate of prey biomass to the predator biomass of the predator y .

Under above stated hypotheses by similar arguments as for Theorem 3.1, we can prove the following:

THEOREM 3.3. Let the hypotheses $H(1, 2, 3^*, 4^*)$, $G(1, 2, 3')$, $P(1, 2^*)$, $S(1, 2^*, 3, 4^*)$ hold. Then the set

$$C = \{(u, x, y, z) : 0 \leq u \leq \tilde{L}, \quad 0 \leq x \leq \tilde{K}, \quad 0 \leq \tilde{c}_1 x + y \leq \tilde{M}, \\ 0 \leq c_2(\tilde{L})x + c_3(\tilde{L})y + z \leq \tilde{N}\}, \quad (3.7)$$

where

$$\begin{aligned} \tilde{K} &= \max_{0 \leq u \leq \tilde{L}} K(u), \quad \tilde{c}_1 = \max_{0 \leq u \leq \tilde{L}} c_1(u), \\ \tilde{M} &= \frac{\tilde{c}_1 \tilde{K}}{\tilde{s}_1} (\alpha g(\tilde{L}, 0) + \tilde{s}_1), \quad \tilde{s}_1 = \min_{0 \leq u \leq \tilde{L}} s_1(u, 0) \\ \tilde{N} &= \frac{1}{s_2(\tilde{L}, 0)} (c_2(\tilde{L}) \tilde{K} (s_2(\tilde{L}, 0) + \alpha g(\tilde{L}, 0)) + c_3(\tilde{L}) \tilde{M} (s_2(\tilde{L}, 0) + \tilde{c}_1 \tilde{p}_1)) \end{aligned} \quad (3.8)$$

and

$$\tilde{p}_1 = \max_{0 \leq u \leq \tilde{L}} p_1(u, \tilde{K}),$$

is positively invariant and attracts all solutions starting with nonnegative initial values.

CHAPTER 4

EXISTENCE, NON-EXISTENCE AND STABILITY OF EQUILIBRIA

In this chapter we shall establish criteria for the existence and non-existence of equilibria of the system (3.1) and discuss their local stability. This information, besides being helpful in understanding the system, will be needed to derive the persistence criteria in later chapters.

4.1 Criteria for the existence and non-existence of equilibria.

It is clear that $E_0(0,0,0,0)$ is an equilibrium for the system (3.1).

THEOREM 4.1. *The system (3.1) has exactly two one-dimensional equilibria, $E_1(L_0, 0, 0, 0)$ and $E_2(0, K_0, 0, 0)$, where $L_0 = L(0, 0, 0)$ and $K_0 = K(0)$.*

PROOF: The subsystem in R_u^+ is given by,

$$u' = uh(u, 0, 0, 0), \quad u(0) > 0. \quad (4.1)$$

Now, from hypothesis (H2) it follows that E_1 is an equilibrium. Furthermore, condition (H1) implies that $\lim_{t \rightarrow \infty} u(t) = L_0$ (see Freedman, 1980), establishing the uniqueness of E_1 . Similar arguments hold for E_2 . The subsystems in R_y^+ and R_z^+ have no equilibria for all of their solutions tend to zero exponentially.

Remark 4.1 It follows from the above arguments that E_0 is stable in the y and z -directions and unstable in the u and x -directions.

THEOREM 4.2. The subsystem in R_{uz}^+ has an equilibrium, $E_3(\bar{u}, \bar{x}, 0, 0)$, provided E_1 and E_2 are unstable in $\overline{R_{uz}^+}$.

PROOF: see (Freedman and Rai, 1987d).

Remark 4.2 As will be seen in the next section (Remark 4.4) because of hypotheses (H1) and (G1), E_3 always exists.

THEOREM 4.3. A necessary and sufficient condition for an equilibrium of the form $E_4(0, x_1, y_1, 0)$, to exist in R_{xy}^+ is that the hypotheses (S3),

$$\exists \hat{x} \ni 0 < \hat{x} < K(0) \text{ and } \frac{s_1(0, 0)}{c_1(0)} = p_1(0, \hat{x}),$$

be satisfied.

PROOF: The solutions of the subsystem

$$\begin{aligned} x' &= \alpha x g(0, x) - y p_1(0, x) \\ y' &= y(-s_1(0, y) + c_1(0) p_1(0, x)), \end{aligned} \tag{4.2}$$

in R_{xy}^+ are bounded for positive time (Freedman, 1980). If (S3) is violated, then from hypotheses (S1), it follows that $\lim_{t \rightarrow \infty} y(t) = 0$, for all solutions initiating in R_{xy}^+ . Thus E_2 is globally stable with respect to R_{xy}^+ . Now suppose (S3) holds. It follows from Theorem 4.1 that E_0 is unstable in the x -direction. Further, (S3) implies that E_2 is unstable in $\overline{R_{xy}^+}$. The result now follows by an application of the Poincaré-Bendixson Theorem.

Similarly, we have the following result:

THEOREM 4.4. A necessary and sufficient condition for equilibrium $E_5(0, x_2, 0, z_2)$ to exist is that,

$$\exists x_0 \ni 0 < x_0 < K(0), \quad \text{and} \quad \frac{s_2(0,0)}{c_2(0)} = p(0, x_0). \quad (4.3)$$

We note that if the food chain in R_{zyx}^+ is simple, E_5 does not exist.

Next, we shall consider the existence of equilibria for the three-dimensional subsystems of (3.1).

THEOREM 4.5. Let the following hypotheses hold for the subsystem in $\overline{R_{uzy}^+}$:

- i) All solutions with nonnegative initial conditions are bounded in forward time.
- ii) E_1 and E_2 are hyperbolic saddle equilibria.
- iii) If E_3 and (or) E_4 exist, they are unique in R_{ux}^+ and (or) R_{xy}^+ , respectively and are unstable in the direction orthogonal to them. Further, let there exist no periodic solution in R_{xy}^+ .

Then there exists an equilibrium, $E_6(u_3, x_3, y_3, 0)$ in R_{uzy}^+ .

PROOF: It follows from Theorem 2.9 that the subsystem is uniformly persistent and thus there exists an equilibrium in R_{uzy}^+ .

Similarly the next two results can be proved.

THEOREM 4.6. Let the hypotheses (i) and (ii) of the above theorem hold for the subsystem in R_{uzy}^+ . Further let E_3 and (or) E_5 if they exist, be unique and

unstable in the y -direction and (or) the u -direction, respectively. If there exist no periodic solutions in R_{xz}^+ , then there exists an equilibrium $E_7(u_4, x_4, 0, z_4)$ in R_{uuz}^+ .

THEOREM 4.7. Let the following hypotheses hold for the subsystem in R_{xyz}^+ :

- (i) All solutions with nonnegative initial conditions are bounded in forward time.
- (ii) E_2 is a hyperbolic saddle point.
- (iii) If E_4 and (or) E_5 exist(s), they are unique and unstable in the z and y -directions, respectively. Further let there exist no periodic solutions in R_{zy}^+ and R_{xz}^+ .

Then there exists an equilibrium, $E_8(0, x_5, y_5, z_5)$ in R_{xyz}^+ .

Remark 4.3 We shall show in Chapter 4, that the Theorems 4.5, 4.6 and 4.7 can hold even when there exists periodic solutions for the two dimensional subsystems.

The following result ensures the non-existence of an interior equilibrium for a three-dimensional subsystem.

THEOREM 4.8. If in system (3.1) a three-dimensional subsystem exhibits extinction, then it does not have an interior equilibrium.

PROOF: Since the subsystem exhibits extinction, the omega limit sets of all solutions of the subsystem initiating with positive initial conditions, converge to

its boundary. This implies that there does not exist an interior equilibrium for the subsystem.

The following result gives a criterion for the existence of an interior equilibrium of the system (3.1).

THEOREM 4.9. *Let the following hypotheses hold for the system (3.1):*

- (i) *all the solutions with nonnegative initial conditions are bounded in forward time,*
- (ii) *the system (3.1) is weakly persistent,*
- (iii) *the subsystems of (3.1) are isolated and acyclic.*

Then an interior equilibrium, $E^*(u^*, x^*, y^*, z^*)$ exists for the system (3.1).

PROOF: See (Butler et al. 1986).

THEOREM 4.10. *The system (3.1) has no interior equilibrium, whenever it exhibits extinction.*

PROOF: Same as for Theorem 4.8.

4.2 Stability of Equilibria

To determine the stability of the various equilibria, we compute the variational matrix of the system (3.1). The signs of the real part of the eigenvalues of

this matrix evaluated at a given equilibrium determine its stability. The variational matrix is given by

$$V(u, x, y, z) = \begin{pmatrix} uh_u + h & uh_x & uh_y & uh_z \\ \alpha x g_u & \alpha x g_x + \alpha g & -p_1 & -p_2 \\ -yp_{1u} - zp_{2u} & -yp_{1x} - zp_{2x} & & \\ y(-s_{1u} + c'_1 p_1 + c_1 p_{1u}) & yc_1 p_{1x} & -s_1 + c_1 p_1 & -q \\ -zq_u & & -ys_{1y} - zq_y & \\ z(-s_{2u} + c'_2 p_2 + c_2 p_{2u} + c'_3 q + c_3 q_u) & zc_2 p_{2x} & zc_3 q_y & -s_2 + c_2 p_2 + c_3 q - zs_{2x} \end{pmatrix} \quad (4.4)$$

The equilibrium $E_0(0,0,0,0)$ has the variational matrix V_0 ,

$$V_0 = V(0,0,0,0) = \begin{pmatrix} h(0,0,0,0) & 0 & 0 & 0 \\ 0 & \alpha g(0,0) & 0 & 0 \\ 0 & 0 & -s_1(0,0) & 0 \\ 0 & 0 & 0 & -s_2(0,0) \end{pmatrix},$$

for which the eigenvalues in the u and x -directions are positive and in the y and z -directions are negative. Thus E_0 has non-empty stable and unstable manifolds.

For the equilibrium $E_1(L_0,0,0,0)$ the variational matrix V_1 , where $L_0 = L(0,0,0)$, is

$$V_1 = \begin{pmatrix} L_0 h_u(L_0,0,0,0) & L_0 h_x(L_0,0,0,0) & L_0 h_y(L_0,0,0,0) & L_0 h_z(L_0,0,0,0) \\ 0 & \alpha g(L_0,0) & 0 & 0 \\ 0 & 0 & -s_1(L_0,0) & 0 \\ 0 & 0 & 0 & -s_2(L_0,0) \end{pmatrix}.$$

There is a positive eigenvalue in the x -direction and negative eigenvalues in the u, y and z directions. Thus E_1 has non-empty stable and unstable manifolds.

Similarly, for equilibrium $E_2(0, K_0, 0, 0)$, where $K_0 = K(0)$, the variational matrix is

$$V_2 = \begin{pmatrix} h(0, K_0, 0, 0) & 0 & 0 & 0 \\ \alpha K_0 g_u(0, K_0) & \alpha K_0 g_z(0, K_0) & -p_1(0, K_0) & -p_2(0, K_0) \\ 0 & 0 & -s_1(0, 0) & 0 \\ 0 & 0 & +c_1(0)p_1(0, K_0) & -s_2(0, 0) \\ & & 0 & +c_2(0)p_2(0, K_0) \end{pmatrix}.$$

Its eigenvalue in the u -direction is positive and in the x -direction is negative.

The eigenvalues in the y and z -directions are,

$$\alpha_i \equiv -s_i(0, 0) + c_i(0)p_i(0, K_0), i = 1, 2. \quad (4.5)$$

Thus α_1 is positive whenever (S3) holds. The eigenvalue in the z -direction may be positive or negative.

Remark 4.4 From the above analysis, it follows that E_1 and E_2 are unstable in $\overline{R_{ux}^+}$. Thus from Theorem 4.2, E_3 always exists. The variational matrix V_3 at the equilibrium point $E_3(\tilde{u}, \tilde{x}, 0, 0)$ is given by

$$V_3 = \begin{pmatrix} \tilde{u}h_u(\tilde{u}, \tilde{x}, 0, 0) & \tilde{u}h_x(\tilde{u}, \tilde{x}, 0, 0) & \tilde{u}h_y(\tilde{u}, \tilde{x}, 0, 0) & \tilde{u}h_z(\tilde{u}, \tilde{x}, 0, 0) \\ \alpha \tilde{x}g_u(\tilde{u}, \tilde{x}) & \alpha \tilde{x}g_z(\tilde{u}, \tilde{x}) & -p_1(\tilde{u}, \tilde{x}) & -p_2(\tilde{u}, \tilde{x}) \\ 0 & 0 & -s_1(\tilde{u}, 0) & 0 \\ 0 & 0 & +c_1(\tilde{u})p_1(\tilde{u}, \tilde{x}) & -s_2(\tilde{u}, 0) \\ & & 0 & +c_2(\tilde{u})p_2(\tilde{u}, \tilde{x}) \end{pmatrix}.$$

The eigenvalues of E_3 are

$$\beta_i \equiv -s_i(\tilde{u}, 0) + c_i(\tilde{u})p_i(\tilde{u}, \tilde{x}), i = 1, 2, \quad (4.6)$$

and $\tilde{\lambda}_{\pm}$, where

$$\tilde{\lambda}_{\pm} = \frac{1}{2}(\tilde{u}h_u + \alpha\tilde{x}g_z) \pm \frac{1}{2}((\tilde{u}h_u + \alpha\tilde{x}g_z)^2 - 4\alpha\tilde{u}\tilde{x}(h_u g_z - g_u h_z))^{1/2},$$

and all the functions are evaluated at $(\tilde{u}, \tilde{x}, 0, 0)$. Thus, whenever $h_u g_z - g_u h_z > 0$, eigenvalues $\tilde{\lambda}_{\pm}$ have negative real parts and E_3 is asymptotically stable in $\overline{R_{u_z}^+}$.

If $h_u g_z - g_u h_z < 0$, E_3 has non-empty stable and unstable manifolds.

Next, the variational matrix and $E_4(0, x_1, y_1, 0)$ is

$$V_4 = \begin{pmatrix} h & 0 & 0 & 0 \\ \alpha x g_u & \alpha x g_z & -p_1 & -p_2 \\ -y p_{1u} & +\alpha g - y p_{1z} & & \\ y(-s_{1u} + c'_1 p_1 + c_1 p_{1u}) & y c_1 p_{1z} & -y s_{1y} & -q \\ 0 & 0 & 0 & -s_2 + c_2 p_2 + c_3 \end{pmatrix},$$

where all the functions are evaluated at $(0, x_1, y_1, 0)$. The eigenvalue in the u -direction, $h(0, x_1, y_1, 0)$, is positive. Thus the equilibrium E_4 is unstable. The eigenvalue in the z -direction is

$$\gamma \equiv s_2(0, 0) + c_2 p_2(0, x_1) + c_3(0) q(0, y_1). \quad (4.7)$$

The other two eigenvalues are the roots of the equation

$$\begin{aligned} \lambda^2 - (\alpha x_1 g_z + \alpha g - y_1 p_{1z} - y s_{1y}) \lambda \\ - y_1 s_{1y} (\alpha x_1 g_z + \alpha g - y_1 p_{1z}) + p_1 y_1 c_1(0) p_{1z} = 0, \end{aligned} \quad (4.8)$$

In case $\frac{\partial s_1(0, y_1)}{\partial y} = 0$, one can use the Rosenzweig and MacArthur criterion (see Freedman, 1980), to determine the stability of E_4 in R_{xy}^+ . In general, from the Routh-Hurwitz criteria, the roots of (4.8) have negative real parts if and only if

$$\alpha x_1 g_z(0, x_1) + \alpha g(0, x_1) - y_1 p_{1z}(0, x_1) - y_1 s_{1y}(0, y_1) < 0,$$

and

$$y_1 s_{1y}(0, y_1)(\alpha x_1 g_z(0, x_1) + \alpha g(0, x_1) - y_1 p_{1z}(0, x_1)) - y_1 c_1(0) p_1(0, x_1) p_{1z}(0, x_1) < 0. \quad (4.9)$$

The variational matrix for $E_5(0, x_2, 0, z_2)$ is given by

$$V_5 = \begin{pmatrix} h & 0 & 0 & 0 \\ \alpha x g_u & \alpha x g_z & -p_1 & -p_2 \\ -z p_{2u} & +\alpha g - z p_{2z} & & \\ 0 & 0 & -s_1 + c_1 p_1 & 0 \\ & & -z q_y & \\ z(-s_{2u} & z c_2 p_{2z} & z c_3 q_y & -z s_{2z} \\ + c'_2 p_2 + c_2 p_{2u}) & & & \end{pmatrix},$$

where all the functions are evaluated at $(0, x_2, 0, z_2)$.

The eigenvalue in the u -direction, $h(0, x_2, 0, z_2)$ is positive and thus E_5 is unstable. The eigenvalue in the y -direction is

$$\delta \equiv s_1(0, 0) + c_1(0) p_1(0, x_2) - z_2 q_y(0, 0). \quad (4.10)$$

The other two eigenvalues have negative real parts if and only if

$$\alpha x_2 g_z(0, x_2) + \alpha g(0, x_2) - z_2 p_{2z}(0, x_2) - z_2 s_{2z}(0, z_2) < 0, \quad (4.11)$$

and

$$z_2 s_{2z}(0, z_2)(\alpha x_2 g_z(0, x_2) + \alpha g(0, x_2) - z_2 p_{2z}(0, x_2)) - z_2 c_2(0) p_2(0, x_2) p_{2z}(0, x_2) < 0. \quad (4.12)$$

The equilibrium $E_6(u_3, x_3, y_3, 0)$ has the variational matrix,

$$V_6 = \begin{pmatrix} u h_u & u h_x & u h_y & u h_z \\ \alpha x g_u & \alpha x g_x & -p_1 & -p_2 \\ -y p_{1u} & +\alpha g - y p_{1z} & & \\ y(-s_{1u} + c'_1 p_1 + c_1 p_{1u}) & y c_1 p_{1z} & -y s_{1y} & -q \\ 0 & 0 & 0 & -s_2 + c_2 p_2 + c_3 q \end{pmatrix},$$

where all the functions are evaluated at $(u_3, x_3, y_3, 0)$.

The eigenvalue in z -direction is

$$\xi \equiv -s_2(u_3, 0) + c_2(u_3, x_3) + c_3(u_3)q(u_3, y_3). \quad (4.13)$$

The other eigenvalues are the zeros of the polynomial

$$\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0, \quad (4.14)$$

where

$$\begin{aligned} a_1 &= u_3 h_u + \alpha x_3 g_x + \alpha g - y_3(p_{1z} + s_{1y}), \\ a_2 &= u_3 h_u (\alpha x_3 g_x + \alpha g - y_3 p_{1z} - y_3 s_{1y}) \\ &\quad + y_3 c_1 p_1 p_{1z} - y_3 s_{1y} (\alpha x_3 g_x + \alpha g - y_3 p_{1z}) \\ &\quad - u_3 h_x (\alpha x_3 g_u - y_3 p_{1u}) - u_3 y_3 h_y (-s_{1u} + c'_1 p_1 + c_1 p_{1u}), \\ a_3 &= u_3 y_3 \{ (\alpha x_3 g_u - y_3 p_{1u})(c_1 h_y p_{1z} - h_x s_{1y}) \\ &\quad - h_u (c_1 p_1 p_{1z} - s_{1y} (\alpha x_3 g_x + \alpha g - y_3 p_{1z})) \\ &\quad + (-s_{1u} + c'_1 p_1 + c_1 p_{1u})(h_y (\alpha x_3 g_x + \alpha g - y_3 p_{1z}) - p_1 h_x) \}. \end{aligned} \quad (4.15)$$

Thus from the Routh-Hurwitz criteria, the necessary and sufficient conditions for E_6 to be asymptotically stable are that $\xi < 0$ and

$$a_1 > 0, \quad a_3 > 0 \text{ and } a_1 a_2 - a_3 > 0. \quad (4.16)$$

Similarly, the variational matrix at $E_7(u_4, x_4, 0, z_4)$ is given by

$$V_7 = \begin{pmatrix} uh_u & uh_x & uh_y & uh_z \\ \alpha x g_u & \alpha x g_x & -p_1 & -p_2 \\ -z p_{2u} & +\alpha g - z p_{2x} & & \\ 0 & 0 & -s_1 + c_1 p_1 & 0 \\ & & -z q_y & \\ z(-s_{2u} & z c_2 p_{2x} & z c_3 q_y & -z s_{2x} \\ + c_2' p_2 + c_2 p_{2u}) & & & \end{pmatrix},$$

where all the functions are evaluated at $(u_4, x_4, 0, z_4)$.

The eigenvalue in y -direction is given by

$$\eta \equiv -s_1(u_4, 0) + c_1(u_4)p_1(u_4, x_4) - z_4 q_y(u_4, 0). \quad (4.17)$$

The other three eigenvalues are the zeros of the polynomial,

$$\lambda^3 + b_1 \lambda^2 + b_2 \lambda + b_3 = 0, \quad (4.18)$$

where

$$\begin{aligned} b_1 &= u_4 h_u + \alpha x_4 g_x + \alpha g - z(p_{2x} + s_{2x}), \\ b_2 &= u_4 h_u (\alpha x_4 g_x + \alpha g - z_4 p_{2x} - z s_{2x}) \\ &\quad + z_4 c_2 p_2 p_{2x} - z_4 s_{2x} (\alpha x_4 g_x + \alpha g - z p_{2x}) \\ &\quad - u_4 h_x (\alpha x_4 g_u - z_4 p_{2u}) + z_4 p_2 (-s_{2u} + c_2' p_2 + c_2 p_{2u}), \\ b_3 &= u_4 z_4 \{ (\alpha x_4 g_u - z_4 p_{2u}) (c_2 h_x p_{2x} - h_x s_{2x}) \\ &\quad - h_u (c_2 p_2 p_{2x} - s_{2x} (\alpha x_4 g_x + \alpha g - z_4 p_{2x})) \\ &\quad + (-s_{2u} + c_2' p_2 + c_2 p_{2u}) (h_x (\alpha x_4 g_x + \alpha g - z_4 p_{2x}) - p_2 h_x) \}. \end{aligned} \quad (4.19)$$

Thus E_7 will be asymptotically stable if and only if $\eta < 0$, and

$$b_1 > 0, \quad b_3 > 0, \quad b_1 b_2 - b_3 > 0. \quad (4.20)$$

Next, the variational matrix for the equilibrium $E_8(0, x_5, y_5, z_5)$ is given by

$$V_8 = \begin{pmatrix} h & 0 & 0 & 0 \\ \alpha x_5 g_u & \alpha x_5 g_x + \alpha g & -p_1 & -p_2 \\ -y_5 p_{2u} - z_5 p_{2u} & -y_5 p_{1x} - z_5 p_{2x} & & \\ y_5(-s_{1u} + c'_1 p_1 + c_1 p_{1u}) - z_5 q_u & y_5 c_1 p_{1x} & -s_1 + c_1 p_1 & -q \\ z_5(-s_{2u} + c'_2 p_2 + c_2 p_{2u} + c'_3 q + c_3 q_u) & z_5 c_2 p_{2x} & z_5 c_3 q_y & -z_5 s_{2x} \end{pmatrix},$$

where all the functions are evaluated at $(0, x_5, y_5, z_5)$.

The eigenvalue in the u -direction, $h(0, x_5, y_5, z_5)$ is positive. Thus the equilibrium is unstable. The other eigenvalues are the zeros of the polynomial

$$\lambda^3 + d_1 \lambda^2 + d_2 \lambda + d_3 = 0, \quad (4.21)$$

where

$$d_1 = \alpha(x_5 g_x + g) - y_5(p_{1x} + s_{1y}) - z_5(p_{2x} + q_y + s_{2x}) - s_2 + c_1 p_1,$$

$$d_2 = z_5(c_3 q q_y - s_{2x}(-s_1 + c_1 p_1 - y_5 s_{1y} - z_5 q_y))$$

$$+ (\alpha x_5 g_x + \alpha g - y_5 p_{1x} - z_5 p_{2x})(-s_1 + c_1 p_1 - y_5 s_{1y} - z_5 q_y - z_5 s_{2x})$$

$$+ (y_5 c_1 p_1 p_{1x} + z_5 c_2 p_2 p_{2x}),$$

$$d_3 = z_5 \{ (y_5 c_1 p_{1x})(p_1 s_{2x} - p_2 c_3 q_y)$$

$$+ c_2 p_{2x}(p_1 q - p_2(-s_1 + c_1 p_1 - y_5 s_{1y} - z_5 q_y))$$

$$- (\alpha x_5 g_x + \alpha g - y_5 p_{1x} - z_5 p_{2x})(c_3 q q_y - s_{2x}(-s_1 + c_1 p_1 - y_5 s_{1y} - z_5 q_y)) \}. \quad (4.22)$$

The equilibrium E_8 will be asymptotically stable in R_{xyz}^+ if and only if

$$d_1 > 0, \quad d_3 > 0, \quad d_1 d_2 - d_3 > 0. \quad (4.23)$$

We shall now consider the stability of the interior equilibrium $E^*(u^*, x^*, y^*, z^*)$.

In what follows, all the functions are assumed to be evaluated at (u^*, x^*, y^*, z^*) .

The variational matrix at E^* is given by

$$V_9 = \begin{pmatrix} u^* h_u & u^* h_x & u^* h_y & u^* h_z \\ \alpha x^* g_u - y^* p_{1u} & \alpha x^* g_x + \alpha g & -p_1 & -p_2 \\ -z^* p_{2u} & -y^* p_{1x} - z^* p_{2x} & & \\ y^* (-s_{1u} + c'_1 p_1 & y^* c_1 p_{1x} & -s_1 + c_1 p_1 & -q \\ + c_1 p_{1u}) - z^* q_u & & -y^* s_{1y} - z^* q_y & \\ z^* (-s_{2u} + c'_2 p_2 & z^* c_2 p_{2x} & z^* c_3 q_y & -z^* s_{2x} \\ + c_2 p_{2u} + c'_3 q + c_3 q_u) & & & \end{pmatrix},$$

Its characteristic polynomial is given by

$$\lambda^4 + A_1 \lambda^3 + A_2 \lambda^2 + A_3 \lambda + A_4 = 0, \quad (4.24)$$

where

$$A_1 = z^* s_{2x} - u^* h_u - f_2 - r_1,$$

$$A_2 = -u^* h_u (z^* s_{2x} - f_2 - r_1) + z^* (c_3 q q_y - s_{2x} r_1 + c_2 p_2 p_{2x})$$

$$- f_2 (z^* s_{2x} - r_1) - y^* c_1 p_1 p_{1x}$$

$$- u^* f_1 h_x - u^* h_y (y^* r_2 - z^* q_u) - u^* z^* r_3 h_x,$$

$$\begin{aligned}
A_3 = & -u^* z^* h_u (c_3 q q_y - s_{2x} r_1 + c_2 p_2 p_{2x}) + u^* h_u f_2 (z^* s_{2x} - r_1) - u^* y^* c_1 h_u p_1 p_{1x} \\
& - z^* [(c_3 q q_y - s_{2x} r_1) f_2 + y^* c_1 p_{1x} (c_3 p_2 q_y - p_1 s_{2x}) - c_2 p_{2x} (p_1 q - r_1 p_2)] \\
& - u^* f_1 [h_x (z^* s_{2x} - r_1) - y^* c_1 h_y p_{1x} - z^* c_2 h_x p_{2x}] \\
& + u^* (y^* r_2 - z^* q_u) [-h_x p_1 - z^* (h_y s_{2x} - c_3 h_x q_y) + f_2 h_y] \\
& - u^* z^* r_3 [h_x p_2 + h_y q - h_x (f_2 + r_1)],
\end{aligned}$$

$$\begin{aligned}
A_4 = & u^* z^* \{ h_u [f_2 (c_3 q q_y - r_1 s_{2x}) + y^* c_1 p_{1x} (c_3 p_2 q_y - p_1 s_{2x}) - c_2 p_{2x} (p_1 q - r_1 p_2)] \\
& - f_1 [h_x (c_3 q q_y - r_1 s_{2x}) - y^* c_1 p_{1x} (h_y s_{2x} - c_3 q_y h_x) \\
& - c_2 p_{2x} (h_y q - r_1 h_x)] \\
& + (y^* r_2 - z^* q_u) [h_x (-p_1 s_{2x} + p_2 c_3 q_y) + f_2 (h_y s_{2x} - c_3 q_y h_x) \\
& + c_2 p_{2x} (p_1 h_x - p_2 h_y)] - r_3 [h_x (p_1 q - r_1 p_2) - f_2 (h_y q - r_1 h_x) \\
& + y c_1 p_{1x} (h_x p_1 - h_y p_2)] \},
\end{aligned} \tag{4.25}$$

and

$$\begin{aligned}
f_1 &= \alpha x^* g_u - y^* p_{1u} - z^* p_{2u}, \\
f_2 &= \alpha x^* g_x + \alpha g - y^* p_{1x} - z^* p_{2x}, \\
r_1 &= -s_1 + c_1 p_1 - y^* s_1 - z^* q_y, \\
r_2 &= -s_{1u} + c'_1 p_1 + c_1 p_{1u}, \\
r_3 &= -s_{2u} + c'_2 p_2 + c_2 p_{2u} + c'_3 q + c_3 q_u.
\end{aligned}$$

Now, using the Routh-Hurwitz Criterion, we have the following result for asymptotic stability of E_9 .

THEOREM 4.11. *A necessary and sufficient condition for the interior equilibrium $E^*(u^*, x^*, y^*, z^*)$ to be asymptotically stable is*

$$A_i > 0, \quad i = 1, 2, 3, 4 \text{ and } A_1 A_2 A_3 - A_3^2 - A_4 A_1^2 > 0. \quad (4.26)$$

The above result signifies that whenever an interior equilibrium exists and is asymptotically stable, there is a region near the equilibrium within which all solutions are attracted to it. Further, we note that conditions (4.23) and (4.26) are independent of each other. This implies that the mutualist's interaction with a food chain can result in both stabilization or destabilization of the system, as has been noted in two and three species models (Addicott and Freedman, 1984; Freedman et al. 1987a). Finally, it shows that the populations feeding on more than one trophic level do not necessarily cause an unstable system, as has been argued by Pimm and Lawton (1978) and that mutualistic interactions can have a significant effect on the stability, even in the case of complex systems.

CHAPTER 5

GLOBAL STABILITY AND PERIODIC SOLUTIONS

In the previous chapter we derived conditions for the asymptotic stability of the various equilibria of the system (3.1). These conditions establish stability relative to small perturbations of initial conditions of the system. However, the real ecosystems are subjected to large perturbations of the initial conditions. In §5.1, we shall derive criteria for the global asymptotic stability of the various boundary equilibria and the interior equilibrium $E^*(u^*, x^*, y^*, z^*)$, whenever it exists. These results ensure stability relative to finite perturbations of the initial conditions of the system. In §5.3, we shall show that the system (3.1) can have periodic solutions.

5.1 Global Asymptotic Stability

It follows from Theorem 4.1, that E_0 is globally asymptotically stable in $\overline{R_{yz}^+}$ and that E_1 and E_2 are globally asymptotically stable in R_u^+ and R_z^+ , respectively. Further, an application of Theorem 2.3, with Dulac function $u^{-1}x^{-1}$ shows that there exist no nontrivial periodic solutions in R_{ux}^+ (Goh, 1980). Thus E_3 is globally asymptotically stable in R_{ux}^+ , whenever it is unique. The conditions for global asymptotic stability of equilibria E_4 and E_5 , in R_{xy}^+ and R_{zx}^+ , respectively, are given in Cheng et al. (1981), Hsu (1978) and Peng and Cheng (1988). Next we consider global stability for the equilibria in the three-dimensional subsystems, whenever they exist.

The subsystems in R_{uzy}^+ and R_{uzy}^+ represent the predator-prey-mutualist systems, as considered in Freedman et al. (1987 a,b). In order to obtain global stability criteria for the equilibrium $E_6(u_3, x_3, y_3, 0)$, we introduce the following notation:

$$\begin{aligned}
 a_{11} &= (u - u_3)h(u, x_3, y_3, 0), \\
 a_{12} &= (u - u_3)[h(u, x, y_3, 0) - h(u, x_3, y_3, 0)] \\
 &\quad + [-s_1(u_3, y_3) + p_1(u_3)p_1(u_3, x)] \\
 &\quad \left[\frac{y(p_1(u_3, x) - p_1(u, x))}{p_1(u_3, x)} + \frac{\alpha x}{p_1(u_3, x)}(g(u, x) - g(u_3, x)) \right], \\
 a_{13} &= (u - u_3)[h(u, x, y, 0) - h(u, x, y_3, 0)] \\
 &\quad (y - y_3)[s_1(u_3, y) - s_1(u, y) - c_1(u_3)p_1(u_3, x) + c_1(u)p_1(u, x)], \\
 a_{22} &= [-s_1(u_3, y_3) + c_1(u_3)p_1(u_3, x)] \left[\frac{\alpha x g(u_3, x)}{p_1(u_3, x)} - y_3 \right], \\
 a_{23} &= 0, \\
 a_{33} &= (y - y_3)[s_1(u_3, y_3) - s_1(u_3, y)]. \tag{5.1}
 \end{aligned}$$

Now we define a symmetric matrix B

$$B(u, x, y) = (b_{ij})_{3 \times 3} \tag{5.2}$$

where the b_{ij} 's are such that

$$\begin{aligned}
 a_{11} &= -b_{11}(u)(u - u_3)^2, & a_{12} &= -2b_{12}(u - u_3)(x - x_3), \\
 a_{13} &= -2b_{13}(u, x, y)(u - u_3)(y - y_3), & a_{22} &= b_{22}(x)(x - x_3), \\
 b_{23} &= 0, & a_{33} &= -b_{33}(y)(y - y_3)^2.
 \end{aligned}$$

THEOREM 5.1. Whenever $B(u, x, y)$, given by (5.2) is positive definite in the region of attraction A_1 of the subsystem in R_{uxy}^+ , E_6 is globally asymptotically stable with respect to solutions initiating in R_{uxy}^+ .

PROOF: See Freedman and Rai (1987a).

Remark 5.1 The set A_1 is given by $\{(u, x, y) : 0 \leq u \leq \tilde{L}, 0 \leq x \leq \tilde{K}, 0 \leq \tilde{c}_1 x + y \leq \tilde{M}\}$, where $\tilde{c}_1, \tilde{L}, \tilde{K}$, and $\tilde{M}$ are given by (3.3), (3.6) or (3.8), depending on the nature of interaction of the mutualist with the food chain. Similarly one can obtain the set A_2 for the next result. In order to obtain the global asymptotic criteria for the equilibrium $E_7(u_4, x_5, 0, z_4)$, we define

$$\begin{aligned} c_{11} &= (u - u_4)h(u, x_4, 0, z_4), \\ c_{12} &= (u - u_4)[h(u, x, 0, z_4) - h(u, x_4, 0, z_4)] + [-s_2(u_4, z_4) + c_2(u_4)p_2(u_4, x)] \\ &\quad \left[\frac{z(p_2(u_4, x) - p_2(u, x))}{p_2(u_4, x)} + \frac{\alpha x}{p_2(u_4, x)}(g(u, x) - g(u_4, x)) \right], \\ c_{13} &= (u - u_4)[h(u, x, 0, z) - h(u, x, 0, z_4)] \\ &\quad + (z - z_4)[s_2(u_4, z) - s_2(u, z) - c_2(u_4)p_2(u_4, x) + c_2(u)p_2(u, x)] \\ c_{22} &= [-s_2(u_4, z_4) + c_2(u_4)p_2(u_4, x)] \left[\frac{\alpha x g(u_4, x)}{p_2(u_4, x)} - z_4 \right], \\ c_{23} &= 0, \\ c_{33} &= (z - z_4)[s_2(u_4, z_4) - s_2(u_4, z)] \end{aligned} \tag{5.3}$$

and

$$D(u, x, z) = (d_{ij})_{3 \times 3}, \tag{5.4}$$

where

$$c_{11} = -d_{11}(u)(u - u_4)^2, \quad c_{12} = -2d_{12}(u, x, z)(u - u_4)(x - x_4),$$

$$c_{13} = -2d_{13}(u, x, z)(u - u_4)(z - z_4), \quad c_{22} = -d_{22}(x)(x - x_4)^2,$$

$$c_{33} = -d_{33}(z)(z - z_4)^2, \quad d_{23} = 0, \quad d_{ij} = d_{ji}.$$

Now we can state the result.

THEOREM 5.2. *Whenever the symmetric matrix $D(u, x, z)$, given by (5.4) is positive definite in the region of attraction A_2 of the subsystem in $R_{u_{zz}}^+$, E_7 is globally asymptotically stable, with respect to solutions initiating in $R_{u_{zz}}^+$.*

PROOF: Same as for Theorem 5.1.

Now we derive a criterion for the global stability of $E_8(0, x_5, y_5, z_5)$ in R_{xyz}^+ .

We remark that such a criterion for a simple food chain has been derived in Freedman and So (1985). We define

$$V(x, y, z) = x - x_5 - x_5 \ln \frac{x}{x_5} + \int_{y_5}^y \frac{Q(x_5, \xi, z_5)}{q(0, \xi)} d\xi + z - z_5 - z_5 \ln \frac{z}{z_5}, \quad (5.5)$$

where

$$Q(x, y, z) = -s_2(0, z) + c_2(0)p_2(0, x) + c_3(0)q(0, y).$$

We note that $V(x_5, y_5, z_5) = 0$ and that $V(x, y, z)$ is positive in $R_{xyz}^+ \setminus \{E_8\}$.

Further $V(x, y, z)$ tends to infinity as x, y or z tend to $0+$ or $+\infty$.

Next we compute $\dot{V}(x, y, z)$, the derivative of $V(x, y, z)$ along the solution of the system (3.1):

$$\begin{aligned}\dot{V} = & (x - x_5)(\alpha g(0, x) - \frac{yp_1(0, x)}{x} - \frac{zp_2(0, x)}{x}) \\ & + Q(x_5, y, z_5)(\frac{y}{q(0, y)}(-s_1(0, y) + c_1(0)p_1(0, x)) - z) \\ & + (z - z_5)Q(x, y, z).\end{aligned}$$

By some algebraic manipulation we can write

$$\dot{V} = \sum_{i=1}^3 \sum_{j=1}^3 e_{ij}, \quad (5.6)$$

where

$$\begin{aligned}e_{11} &= (x - x_5)(\alpha g(0, x) - y_5 \frac{p_1(0, x)}{x} - z_5 \frac{p_2(0, x)}{x}) \\ e_{12} &= -(x - x_5)(y - y_5) \frac{p_1(0, x)}{x} \\ &\quad + c_1(0)Q(x_5, y, z_5)(p_1(0, x) - p_1(0, x_5)) \frac{y}{q(0, y)}, \\ e_{13} &= -(x - x_5)(z - z_5) \frac{p_2(0, x)}{x} + c_2(0)(z - z_5)(p_2(0, x) - p_2(0, x_5)), \\ e_{22} &= Q(x_5, y, z_5)(-\frac{ys_1(0, y)}{q(0, y)} + c_1(0) \frac{yp_1(0, x_5)}{q(0, y)} - z_5) \\ e_{23} &= -(z - z_5)Q(x_5, y, z_5) + c_3(0)(z - z_5)(q(0, y) - q(0, y_5)), \\ e_{33} &= (z - z_5)(s_2(0, z_5) - s_2(0, z)).\end{aligned} \quad (5.7)$$

Further we define a symmetric matrix

$$\mathcal{F}(x, y, z) = (f_{ij})_{3 \times 3}, \quad (5.8)$$

such that

$$e_{11} = -f_{11}(x)(x - x_5)^2, \quad e_{12} = -2f_{12}(x, y)(x - x_5)(y - y_5),$$

$$e_{13} = -2f_{13}(x, z)(x - x_5)(z - z_5), \quad e_{22} = -f_{22}(y)(y - y_5)^2,$$

$$e_{23} = -2f_{23}(y, z)(y - y_5)(z - z_5), \quad e_{33} = -f_{33}(z)(z - z_5)^2.$$

We can now prove the following:

THEOREM 5.3. *Let the matrix $\mathcal{F}(x, y, z)$ be positive definite in the region of attraction A_3 ,*

$$A_3 = \{(x, y, z) : 0 \leq x \leq K_0, 0 \leq c_1(0)x + y \leq M, \\ 0 \leq c_2(0)x + c_3(0)y + z \leq N\}, \quad (5.9)$$

where

$$K_0 = K(0), \quad M = \frac{c_1(0)K_0}{s_2(0,0)}(\alpha g(0,0) + s_1(0,0)),$$

$$N = \frac{1}{s_2(0,0)}(c_2(0)K_0(s_2(0,0) + \alpha g(0,0)) + c_3(0)M(s_2(0,0) + c_1(0)p_1(0, K_0))).$$

Then the equilibrium $E_8(0, x_5, y_5, z_5)$ is globally asymptotically stable with respect to solutions initiating in R_{xyz}^+ .

PROOF: It can be shown by arguments similar to those in Theorem 3.1 that the set A_3 defines a region of attraction for the food chain. Further, as $\mathcal{F}(x, y, z)$ is positive definite in A_3 , it follows from (5.6) and (5.8) that

$$\dot{V} = -p\mathcal{F}p^T \leq 0,$$

where $p = (x - x_5, y - y_5, z - z_5)$. Thus $V(x, y, z)$ defines a Lyapunov function.

Finally as the set $\{(x, y, z) \in R_{xyz}^+ : \dot{V} = 0\}$ is precisely $\{E_8\}$, we conclude that

E_8 is globally asymptotically stable (see Hale (1969)).

Remark 5.1 A necessary condition for $\mathcal{F}(x, y, z)$ to be positive definite is, $f_{11} > 0$, $i = 1, 2, 3$. It is clear that f_{23} is always positive. But $f_{11} > 0$ if and only if

$$(x - x_5)(\alpha g(0, x) - y_5 \frac{p_1(0, x)}{x} - z_5 \frac{p_2(0, x)}{x}) < 0, \quad 0 < x < K_0, \quad x \neq x_5.$$

This can be interpreted geometrically as a requirement that x_5 must lie to the right of local maxima (if any), of the function $z = \frac{\alpha x g(0, x) - y_5 p_1(0, x)}{p_2(0, x)}$ and y_5 lie below all local minima (if any). Further $f_{22} > 0$ if

$$(y - y_5)(\frac{y s_1(0, y)}{q(0, y)} + c_1(0) \frac{y p_1(0, x_5)}{q(0, y)} - z_5) < 0, \quad 0 < y < M, \quad y \neq y_5. \quad (5.10)$$

This implies that we must have

$$\frac{q(0, y)}{y} < \frac{q(0, y_5)}{y_5} \quad \text{if } 0 < y < y_5, \quad (5.11)$$

and the reverse inequality for $y_5 < y < M$. As observed by Freedman and So (1985), this could be satisfied if $q(0, y)$ is a Holling type-III (sigmoid) function.

Lastly, we derive a criterion for the global asymptotic stability of the interior equilibrium $E^*(u^*, x^*, y^*, z^*)$, with respect to the solutions initiating in the positive orthant R_{uzyz}^+ . We remark that the criterion of uniform persistence, derived in later chapters ensures the existence of E^* . We define $V(u, x, y, z)$ by

$$V(u, x, y, z) = V_1(u) + V_2(x) + V_3(y) + V_4(z), \quad (5.12)$$

where

$$V_i(p) = p - p^* \ln \frac{p}{p^*}, \quad i = 1, 2, 4$$

and

$$V_i(y) = \int_{y^*}^y \frac{R(u^*, x^*, \xi, z^*)}{q(u^*, \xi)} d\xi,$$

$$R(u, x, y, z) = -s_2(u, z) + c_2(u)p_2(u, x) + c_3(u)q(u, y).$$

Then $V(u^*, x^*, y^*, z^*) = 0$ and $V(u, x, y, z)$ is positive definite about (u^*, x^*, y^*, z^*) .

Further each $V_i(p)$ tends to ∞ as $p \rightarrow 0+$ or ∞ . Now we shall compute $\dot{V}$, the derivative of $V(u, x, y, z)$ along the solution of the system (3.1):

$$\dot{V}(u, x, y, z) = V'_1(u)\dot{u} + V'_2(x)\dot{x} + V'_3(y)\dot{y} + V'_4(z)\dot{z}, \quad (5.13)$$

where

$$V'_i(p) = \frac{p - p^*}{p}, \quad i = 1, 2, 4,$$

and

$$V'_3(y) = \frac{R(u^*, x^*, y, z^*)}{q(u^*, y)}.$$

Using (3.1) in (5.13), after some algebraic manipulations, we can write

$$\dot{V} = \sum_{i=1}^4 \sum_{j=1}^4 \ell_{ij}, \quad (5.14)$$

where

$$\ell_{11} = (u - u^*)h(u, x^*, y^*, z^*),$$

$$\begin{aligned}
\ell_{12} &= (u - u^*)[h(u, x, y, z) - h(u, x^*, y, z)] \\
&\quad + (x - x^*)[\alpha g(u, x) - y^* \frac{p_1(u, x)}{x} - z^* \frac{p_2(u, x)}{x} - \alpha g(u^*, x) \\
&\quad + y^* \frac{p_1(u^*, x)}{x} + z^* \frac{p_2(u^*, x)}{x}], \\
\ell_{13} &= (u - u^*)[h(u, x^*, y, z) - h(u, x^*, y^*, z)] \\
&\quad + R(u^*, x^*, y, z^*)[z - \frac{ys_1(u, y)}{q(u^*, y)} + c_1(u) \frac{yp_1(u, x)}{q(u^*, y)} \\
&\quad - \frac{zq(u, y)}{q(u^*, y)} + \frac{ys_1(u^*, y)}{q(u^*, y)}] - c_1(u^*) \frac{yp_1(u^*, x)}{q(u^*, y)}, \\
\ell_{14} &= (u - u^*)[h(u, x^*, y^*, z) - h(u, x^*, y^*, z^*)] + (z - z^*)[R(u, x, y, z) - R(u^*, x, y, z)],
\end{aligned}
\tag{5.15}$$

$$\begin{aligned}
\ell_{22} &= (x - x^*)[\alpha g(u^*, x) - y^* \frac{p_1(u^*, x)}{x} - z^* \frac{p_2(u^*, x)}{x}], \\
\ell_{23} &= -(x - x^*)(y - y^*) \frac{p_1(u, x)}{x} + c_1(u^*) R(u^*, x^*, y, z^*) [\frac{yp_1(u^*, x)}{q(u^*, y)} - \frac{yp_1(u^*, x^*)}{q(u^*, y)}], \\
\ell_{24} &= -(x - x^*)(z - z^*) \frac{p_2(u, x)}{x} + (z - z^*) c_2(u) [p_2(u^*, x) - p_2(u^*, x^*)], \\
\ell_{33} &= R(u^*, x^*, y, z^*) [-\frac{ys_1(u^*, y)}{q(u, y)} + c_1(u^*) \frac{yp_1(u^*, x^*)}{q(u^*, y)} - z^*], \\
\ell_{34} &= -(z - z^*) R(u^*, x^*, y, z^*) + (z - z^*) c_3(u^*) [q(u^*, y) - q(u^*, y^*)]
\end{aligned}$$

and

$$\ell_{44} = (z - z^*)[s_2(u^*, z^*) - s_2(u^*, z)].$$

We now define a symmetric matrix,

$$M(u, x, y, z) = (m_{ij})_{4 \times 4}, \tag{5.16}$$

where

$$\ell_{11} = -m_{11}(u)(u - u^*)^2, \ell_{12} = 2m_{12}(u, x, y, z)(u - u^*)(x - x^*),$$

$$\ell_{13} = -2m_{13}(u, x, y, z)(u - u^*)(y - y^*),$$

$$\ell_{14} = -2m_{14}(u, x, y, z)(u - u^*)(z - z^*),$$

$$\ell_{22} = -m_{22}(x)(x - x^*)^2, \quad \ell_{23} = -2m_{23}(u, x, y)(x - x^*)(y - y^*),$$

$$\ell_{24} = -2m_{24}(u, x, z)(x - x^*)(z - z^*), \quad \ell_{33} = -m_{33}(y)(y - y^*)^2,$$

$$\ell_{34} = -2m_{34}(u, z)(y - y^*)(z - z^*), \quad \ell_{44} = -m_{44}(z)(z - z^*)^2.$$

Now we can state the following result:

THEOREM 5.4. *Whenever the matrix $M(u, x, y, z)$ is positive definite in the region of attraction A of the system (3.1), the interior equilibrium $E^*(u^*, x^*, y^*, z^*)$ is globally asymptotically stable with respect to solutions initiating in the positive orthant R_{uxyz}^+ .*

PROOF: Same as Theorem 5.3.

Remark 5.2 A necessary condition for the matrix $M(u, x, y, z)$ to be positive definite is that $m_{ii} > 0$, $i = 1, 2, 3, 4$, in A . The elements m_{11} and m_{44} are always positive. As in Remark 5.1, one can obtain criteria for m_{22} and m_{33} to be positive.

We now illustrate the above analysis with an example. The following system of differential equations models a mutualist's interaction with a Lotka-Volterra

food chain:

$$\begin{aligned}
 u' &= \alpha u \left(1 - \frac{u}{L + \ell y}\right), \\
 x' &= x \left(1 - \frac{x}{K}\right) - \gamma_0 xy - \delta_0 xz, \\
 y' &= y(-s_{10} + s_{11}u - s_{12}y + c_1\gamma_0x) - \xi_0 yz, \\
 z' &= z(-s_{20} - s_{22}z + c_2\delta_0x + c_3\xi_0y),
 \end{aligned} \tag{5.17}$$

where all the constants are positive. The mutualism exists and is obligate for the predator y , whenever $\ell > 0$, $s_{11} > 0$ and $Kc_1\gamma_0 \leq s_{10}$. With $\alpha = \frac{1}{10}$, $L = 3$, $\ell = \frac{3}{4}$, $K = 2$, $\gamma_0 = \frac{1}{4}$, $\delta_0 = \xi_0 = c_1 = \frac{1}{2}$, $s_{10} = s_{11} = s_{12} = s_{22} = \frac{1}{3}$, $s_{20} = \frac{1}{6}$, $c_2 = c_3 = 1$, (5.17) has an interior equilibrium $E^*(\frac{117}{32}, \frac{3}{10}, \frac{7}{8}, \frac{101}{80})$. The region of attraction is contained in

$$A = \{0 \leq u \leq \frac{45}{2}, 0 \leq x \leq 2, 0 \leq y \leq 11, 0 \leq z \leq 19\}.$$

Finally, the matrix $M(u, x, y, z)$ as defined by (5.16) is

$$\begin{pmatrix} \frac{16}{585} & 0 & -\frac{1}{6} & 0 \\ 0 & \frac{1}{2} & \frac{1}{16} & \frac{1}{8} \\ -\frac{1}{6} & \frac{1}{16} & \frac{1}{3} & 0 \\ 0 & \frac{1}{8} & 0 & \frac{1}{3} \end{pmatrix},$$

which is positive definite. Thus from Theorem 5.4, E^* is globally asymptotically stable with respect to solutions initiating in R_{uzyz}^+ .

5.2 Periodic Solutions

In the case of two species mutualism, the Kolmogorov model does not admit any non-trivial periodic solutions (Albrecht et al. 1974, Freedman et al. 1982). In case of a mutualist-predator-prey system Rai et al. (1983) showed that Hopf-bifurcation can occur. Below we derive conditions under which Hopf-bifurcation

occurs in the system (3.1), for a certain value α_0 of the bifurcation parameter α . For this we need to assume that the interior equilibrium $E^*(u^*, x^*, y^*, z^*)$ exists. We remark that uniform persistence, for example, implies that E^* exists (Theorem 4.9).

The characteristic polynomial of E^* is given by

$$P(\lambda) \equiv \lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4 = 0, \quad (5.18)$$

where $A_i, i = 1, 2, 3, 4$ are given by (4.25) and are functions of the parameter α .

Define the third order Hurwitz determinant,

$$\Delta_3(\alpha) = [A_1(\alpha)A_2(\alpha) - A_3(\alpha)]A_3(\alpha) - A_1^2(\alpha)A_4(\alpha). \quad (5.19)$$

THEOREM 5.5. Suppose there exists $\alpha_0 > 0$ such that $A_i(\alpha_0) > 0$, $\Delta_3(\alpha_0) = 0$ and

$$\left[(A_1A_2 - 2A_3)\left(A_3\frac{dA_1}{d\alpha} - A_1\frac{dA_3}{d\alpha}\right) + A_1^2\left(A_1\frac{dA_4}{d\alpha} - A_3\frac{dA_2}{d\alpha}\right) \right]_{\alpha=\alpha_0} \neq 0. \quad (5.20)$$

Then the equilibrium E^* bifurcates into small amplitude periodic solutions as α passes through α_0 . Furthermore, there exists a neighbourhood U of E^* such that any closed orbit in U is one of the above periodic solutions.

PROOF: We will show that conditions of Hopf bifurcation theorem are satisfied. First we show that for $\alpha = \alpha_0$, $P(\lambda)$ has two imaginary roots and that the other roots have negative real parts.

From the Orlando formula

$$\Delta_3(\alpha) = \prod_{\substack{i,j=1,2,3,4 \\ i < j}} (\lambda_i + \lambda_j), \quad (5.21)$$

where $\lambda_i, i = 1, 2, 3, 4$ are the roots of $P(\lambda)$. Thus a necessary and sufficient condition for the sum of two roots of $P(\lambda)$ to be zero is that $\Delta_3(\alpha)$ must be zero. Therefore when $\alpha \equiv \alpha_0$, $P(\lambda)$ has two roots λ_1 and $-\lambda_1$. Further, λ_1 is purely imaginary, for otherwise

$$\lambda_1^4 + A_1 \lambda_1^3 + A_2 \lambda_1^2 + A_3 \lambda_1 + A_4 = 0$$

and

$$\lambda_1^4 - A_1 \lambda_1^3 + A_2 \lambda_1^2 - A_3 \lambda_1 + A_4 = 0$$

yield

$$A_1(\alpha_0) \lambda_1^3 + A_3(\alpha_0) \lambda_1 = 0,$$

which contradicts $A_1(\alpha_0) A_3(\alpha_0) > 0$. Since $A_1(\alpha_0) > 0$ and $A_4(\alpha_0) > 0$, the sum of the roots of $P(\lambda)$ is negative and their product is positive. Thus the remaining two roots of $P(\lambda)$ have negative real parts.

Finally, we need to show that $\operatorname{Re} \frac{d\lambda_1(\alpha)}{d\alpha} \Big|_{\alpha=\alpha_0} \neq 0$. For this let

$$\lambda_1(\alpha) = \mu(\alpha) = i\nu(\alpha). \quad (5.22)$$

Now differentiating equation (5.18) with respect to α and setting α equal to α_0 , we obtain

$$\begin{aligned} & [-3A_1(\alpha_0)\nu^2(\alpha_0) + A_3(\alpha_0)] \frac{d\mu(\alpha_0)}{d\alpha} - [-4\nu^3(\alpha_0) + 2A_2(\alpha_0)\nu(\alpha_0)] \frac{d\nu(\alpha_0)}{d\alpha} \\ & = \nu^2(\alpha_0) \frac{dA_2(\alpha_0)}{d\alpha} - \frac{dA_4(\alpha_0)}{d\alpha}, \end{aligned}$$

and

$$\begin{aligned} & [-4\nu^2(\alpha_0) + 2A_2(\alpha_0)\nu(\alpha_0)] \frac{d\mu(\alpha_0)}{d\alpha} - [-3A_1(\alpha_0)\nu^2(\alpha_0) + A_3(\alpha_0)] \frac{d\nu(\alpha_0)}{d\alpha} \\ & = \nu^3(\alpha_0) \frac{dA_1(\alpha_0)}{d\alpha} - \nu(\alpha_0) \frac{dA_3(\alpha_0)}{d\alpha}. \end{aligned}$$

Solving for $\frac{d\mu(\alpha_0)}{d\alpha}$, we get

$$\begin{aligned} \frac{d\mu(\alpha_0)}{d\alpha} &= (-3A_1\nu^2 + A_3)(\nu^2 A_2' - A_4') \\ &+ \left[\frac{(4\nu^3 + 2A_2\nu)(\nu^3 A_1' - \nu A_3')}{(-3A_1\nu^2 + A_3)^2 + (-4\nu^3 + 2A_2\nu)^2} \right]_{\alpha=\alpha_0} \end{aligned} \quad (5.23)$$

Further at $\alpha = \alpha_0$ equation (5.18) yields

$$\nu^4(\alpha_0) - A_2(\alpha_0)\nu^2(\alpha_0) + A_4(\alpha_0) = 0,$$

and

$$-A_4(\alpha_0)\nu^3(\alpha_0) + A_3(\alpha_0)\nu(\alpha_0) = 0,$$

from which we conclude

$$\nu^2(\alpha_0) = \frac{A_3(\alpha_0)}{A_1(\alpha_0)}.$$

Now from (5.23) we obtain

$$\frac{d\mu}{d\alpha} \Big|_{\alpha=\alpha_0} = \frac{\{(A_1 A_2 - 2A_3)(A_3 \frac{dA_1}{d\alpha} - A_1 \frac{dA_3}{d\alpha}) + A_1^2 (A_1 \frac{dA_4}{d\alpha} - A_3 \frac{dA_2}{d\alpha})\}}{2\{A_1^3 A_3 + (A_1 A_2 - 2A_3)^2\}} \Big|_{\alpha=\alpha_0} \neq 0,$$

which completes the proof.

Now we illustrate the existence of periodic solutions with an example. The system we consider is

$$u' = \gamma u \left(1 - \frac{u}{L + \ell y}\right),$$

$$x' = \alpha x \left(1 - \frac{x}{K}\right) - \gamma_0 xy,$$

$$y' = y(-s_{10} - s_{11}u + c_1\gamma_0x) - \frac{\delta_0 yz}{1 + mu},$$

$$z' = z(-s_{20} - s_{21}z + \frac{c_2\delta_0}{1 + mu}y),$$

where all the constants are positive.

This system exhibits facultative mutualism between the mutualist u and predator y . When $\gamma = \frac{1}{2}$, $L = 2$, $\ell = 0.10$, $K = 5$, $\gamma_0 = \frac{3}{4}$, $s_{10} = s_{11} = 0.10$, $c_1 = \delta_0 = 1$, $m = s_{20} = s_{21} = 0.20$, $c_2 = \frac{3}{4}$ bifurcation occurs at $\alpha_0 = 2.23$ approximately, giving "small amplitude" periodic solution. Here $u^* = 2.136$, $x^* = 2.717$, $y^* = 1.359$, $z^* = 2.571$, approximately.

CHAPTER 6

FACULTATIVE MUTUALISM WITH THE PREY

We now address the question of persistence versus extinction of the populations of our system. Specifically, in §6.2 we derive criteria which ensure the uniform persistence of the system (3.1), in the case of facultative mutualism between the mutualist u and the prey x . In §6.4 we show that the system (3.1) can in fact reverse the outcome exhibited by its three-dimensional subsystem.

6.1 Preliminaries

The system (3.1) exhibits facultative mutualism between the mutualist u and the prey x whenever the hypotheses $H(1-4)$, $G(1,2)$, $P(1,2)$ and $S(1-3)$ are satisfied (§3.2).

We recall the following notation from Chapter 4.

The eigenvalue of $E_2(0, K(0), 0, 0)$ in the z -direction is

$$\alpha_1 \equiv -s_2(0, 0) + c_2(0)p_2(0, K(0)). \quad (6.1)$$

The eigenvalues of $E_3(u_3, x_3, 0, 0)$ in the y and z -directions are

$$\beta_i \equiv -s_i(\tilde{u}, 0) + c_i(\tilde{u})p_i(\tilde{u}, \tilde{x}), \quad i = 1, 2. \quad (6.2)$$

The eigenvalues of $E_4(0, x_1, y_1, 0)$ and $E_5(0, x_2, 0, z_2)$ (whenever they exist) in the z and y -directions are

$$\gamma \equiv -s_2(0, 0) + c_2(0)p_2(0, x_1) + c_3(0)q(0, y_1), \quad (6.3)$$

and

$$\delta \equiv -s_1(0,0) + c_1(0)p_1(0,x_2) - z_2q_y(0,0), \quad (6.4)$$

respectively.

The eigenvalues of $E_6(u_3, x_3, y_3, 0)$, $E_7(u_4, x_4, 0, z_4)$ and $E_8(0, x_5, y_5, z_5)$ (whenever they exist) in the z, y and u -directions are ξ, η and ν respectively, where

$$\xi \equiv -s_2(u_3, 0) + c_2(u_3)p_2(u_3, x_3) + c_3(u_3)q(u_3, y_3), \quad (6.5)$$

$$\eta \equiv -s_1(u_4, 0) + c_1(u_4)p_1(u_4, x_4) - z_4q_y(u_4, 0), \quad (6.6)$$

and

$$\nu \equiv h(0, x_5, y_5, z_5). \quad (6.7)$$

We observe that by (H1) ν is always positive.

From Theorem 4.1 and Theorem 4.2 we obtain that the equilibria E_0, E_1, E_2 and E_3 always exist. Hypothesis (S3) and Theorem 4.3 together imply that E_4 exists. The equilibrium E_5 exists whenever $\alpha_1 > 0$.

Finally as the system (3.1) has a compact region of attraction (see Theorem 3.1), we conclude that (3.1) is a dissipative system.

6.2 Uniform Persistence

In this section we give criteria for uniform persistence in the three-dimensional subsystems and the system (3.1). For the sake of simplicity we always assume that the boundary equilibria (whenever they exist) are unique.

Now we introduce the following hypothesis:

(H5) Let the equilibrium E_4 be globally asymptotically stable with respect to solutions initiating in R_{zy}^+ .

(H6) Let E_5 (if it exists) be globally asymptotically stable with respect to solutions initiating in R_{xz}^+ .

The following result holds for the food chain in R_{xyz}^+ .

THEOREM 6.1. *Let hypotheses $G(1,2)$, $P(1,2)$, $S(1-3)$ and $H(5,6)$ hold. Then the subsystem in R_{xyz}^+ is uniformly persistent whenever $\gamma > 0$ and $\delta > 0$.*

PROOF: The proof is similar to the one given by Freedman and So (1985) in the case of a simple food chain.

In the absence of the top-predator z , the system (3.1) reduces to a predator-prey-mutualist system and we have the following:

THEOREM 6.2. *Let hypotheses $H(1-5)$, $G(1,2)$, $P(1,2)$ and $S(1-3)$ hold. Then the three-dimensional subsystem in R_{uxy}^+ is uniformly persistent, whenever $\beta_1 > 0$.*

PROOF: See Freedman and Rai (1987a).

Similarly one can prove the following:

THEOREM 6.3. *Let hypotheses $H(1-4,6)$, $G(1,2)$, $P(1,2)$ and $S(1,2)$ hold. Then the three-dimensional subsystem in R_{uwx}^+ is uniformly persistent, whenever $\beta_2 > 0$.*

The hypotheses $H(5,6)$ exclude the possibility of periodic orbits for the predator-prey systems in R_{xy}^+ and R_{zx}^+ . In the case of a simple food chain, Freedman and Waltman (1977) showed that weak persistence can hold even when there exist a finite number of limit cycles. Below we obtain a criterion for uniform persistence for the food chain in R_{xyz}^+ when periodic solutions exist.

THEOREM 6.4. *Let hypotheses $G(1,2)$, $P(1,2)$ and $S(1-3)$ hold. Further let there exist a finite number of periodic solutions $x = \phi_i(t)$, $y = \psi_i(t)$, $i = 1, 2, \dots, k$ and $x = \xi_j(t)$, $z = \eta_j(t)$, $j = 1, 2, \dots, \ell$ in R_{xy}^+ and R_{zx}^+ , respectively. Then the food chain in R_{xyz}^+ is uniformly persistent, provided $\gamma > 0$, $\delta > 0$ and for each periodic solution of period T in R_{xy}^+ ,*

$$m_i = -s_2(0,0) + \frac{1}{T} \int_0^T [c_2(0)p_2(0, \phi_i(t)) + c_3(0)q(0, \psi_i(t))] dt > 0, \quad i = 1, 2, \dots, k, \quad (6.8)$$

and for each periodic solution $(\xi_j(t), \eta_j(t))$ of period ω in R_{zx}^+ ,

$$\eta_j = -s_1(0,0) + \frac{1}{\omega} \int_0^\omega [c_1(0)p_1(0, \xi_j(t)) - q_y(0,0)\eta_j(t)] dt > 0, \quad j = 1, 2, \dots, \ell, \quad (6.9)$$

PROOF: For any $x \in R_{xyz}^+$, let $O(x)$ denote the orbit through x and $\Omega(x)$ be its omega-limit set. From Theorem 5.3, we conclude that $\Omega(x)$ is bounded.

We claim that $E_0 \notin \Omega(x)$. If $E_0 \in \Omega(x)$, then by the Butler-McGehee Lemma there exists a point P in $\Omega(x) \cap W^s(E_0)$. Since $O(P)$ lies in $\Omega(x)$ and $W^s(E_0)$ is $\overline{R_{yz}^+}$, we conclude that $O(P)$ is unbounded, which is a contradiction.

Next $E_2 \notin \Omega(x)$, for otherwise since E_2 is a saddle point, by the Butler-McGehee Lemma there exists a point P in $\Omega(x) \cap W^s(E_2)$. Now $W^s(E_2) = R_z^+$ implies that either $E_0 \in \Omega(x)$ or an unbounded orbit lies in $\Omega(x)$. In either case the result is a contradiction.

Now we show that no periodic orbit in R_{xy}^+ or E_4 belongs to $\Omega(x)$. Let γ_i , $i = 1, 2, \dots, k$ denote the closed orbit of the periodic solution $(\phi_i(t), \psi_i(t))$ in R_{xy}^+ such that γ_i lies inside γ_{i-1} .

The variational matrix $V_i(\phi_i(t), \psi_i(t), 0)$ corresponding to γ_i is given by

$$V_i = \begin{bmatrix} g(0, \phi_i(t)) + \phi_i(t)g_z(0, \phi_i(t)) & -p_1(0, \phi_i(t)) & -p_2(0, \phi_i(t)) \\ -\psi_i(t)p_{1z}(0, \phi_i(t)) & & \\ c_1(0)\psi_i(t)p_{1z}(0, \phi_i(t)) & -s_1(0, \psi_i(t)) & -q(0, \psi_i(t)) \\ & +c_1(0)p_1(0, \phi_i(t)) & \\ & -\psi_i(t)s_{1y}(0, \psi_i(t)) & \\ 0 & 0 & -s_2(0, 0) \\ & & +c_2(0)p_2(0, \phi_i(t)) \\ & & +c_3(0)q(0, \psi_i(t)) \end{bmatrix}.$$

Computing the fundamental matrix of the linear periodic system

$$X' = V_i(t)X, \quad X(0) = I, \quad (6.10)$$

we find that its Floquet multiplier in the z -direction is $e^{m_i T}$.

Suppose γ_1 lies in $\Omega(x)$. Then from (6.8) its Floquet multiplier in the z -direction is greater than one and therefore by Theorem 2.10 there exists a point $P_1 \in W^s(\gamma_1) \cap \Omega(x)$. If P_1 lies outside γ_1 then $\mathcal{O}(P)$ lies in $\Omega(x)$ and is unbounded, which is a contradiction. If γ_1 is stable from inside then $\Lambda(P_1)$ must be γ_2 and is contained in $\Omega(x)$. If γ_2 is unstable from the inside as well, we have a contradiction, for a repeller cannot be in $\Omega(x)$. If γ_2 is stable from the inside, again from Theorem 2.10 there exists a point P_2 inside γ_2 such that $P_2 \in W^s(\gamma_2) \cap \Omega(x)$. Continuing this argument we get that either γ_1 is unstable from both sides or it is stable from inside and there exists a point P_k in $W^s(\gamma_1) \cap \Omega(x)$. If such a P_k exists then E_4 must be a repeller and $\Lambda(P_k) = E_4$ lies in $\Omega(x)$, which is again a contradiction. Thus γ_1 does not lie in $\Omega(x)$. By similar arguments we obtain that no γ_i lies in $\Omega(x)$.

Repeating the above steps we also conclude that no closed orbit in R_{xz}^+ or E_5 lies in $\Omega(x)$. Thus $\Omega(x)$ lies in R_{xyz}^+ and the subsystem in R_{xyz}^+ is persistent. Finally, since only the closed orbits and the equilibria form the omega limit set of the solutions on the boundary of R_{xyz}^+ , Theorem 2.9 implies that the food chain is uniformly persistent.

Remark 6.1 In case there are no periodic solutions in R_{xz}^+ or if E_5 does not exist, the above theorem holds without assuming inequality (6.9).

Remark 6.2 For the predator-prey-mutualist system in $R_{uzy}^+(R_{uiz}^+)$ Theorem 6.2 (6.3) holds even without hypothesis $H5(H6)$. This is so because the

Floquet multiplier of any closed orbit $(\phi(t), \psi(t))$ of period T in $R_{xy}^+(R_{xz}^+)$ in the u -direction is $e^{\int_0^T \lambda(0, \phi(t), \psi(t), 0) dt}$ and is always greater than one by hypothesis (H1).

Next we derive a criterion for the uniform persistence of the system (3.1), when all its three-dimensional subsystems possess an interior equilibrium. We recall that whenever a subsystem of (3.1) is uniformly persistent it has an interior equilibrium (Theorem 4.9). First we introduce the following hypothesis:

(H7) Let the equilibrium E_6, E_7 and E_8 be globally asymptotically stable in R_{xy}^+, R_{xz}^+ and R_{yz}^+ , respectively.

THEOREM 6.5. *Let hypotheses $H(1-4, 7)$, $G(1, 2)$, $P(1, 2)$ and $S(1-3)$ hold. Further, let either $H(5, 6)$ or inequalities (6.8) and (6.9) hold. Then the system (3.1) is uniformly persistent, whenever $\xi > 0$ and $\eta > 0$.*

PROOF: Let $O(x)$ be an orbit through any point $x \in R_{xyz}^+$. Then from Theorem 3.1 its omega limit set, $\Omega(x)$ is bounded. Also from the previous theorems it follows that the three-dimensional subsystems are uniformly persistent. Now we show that no boundary equilibria belong to $\Omega(x)$. Suppose E_0 belongs to $\Omega(x)$. Since E_0 is a saddle point, by the Butler-McGehee Lemma there exists a point P in $\Omega(x) \cap W^s(E_0)$. Further as $W^s(E_0)$ is precisely $\overline{R_{yz}^+}$, $O(P)$ is unbounded and lies in $\Omega(x)$, which is a contradiction.

$E_1 \notin \Omega(x)$. Otherwise by the Butler-McGehee Lemma there exists at least one point $P \in \Omega(x) \cap W^s(E_1)$. However, as $W^s(E_1)$ is $\overline{R_{yz}^+}/\overline{R_{yz}^+}$ if $P \in R_u^+$,

then either $\Delta(P) = E_0$ belongs to $\Omega(x)$ or $O(P)$ is unbounded and lies in $\Omega(x)$.

Both of these statements are contradictions. Otherwise $P \in R_{uy}^+ \cup R_{ux}^+ \cup R_{uyz}^+$ and again $O(P)$ is unbounded and lies in $\Omega(x)$ contradicting the boundedness of $\Omega(x)$.

Next we show that E_3 cannot be in $\Omega(x)$. Since there are no periodic orbits in R_{ux}^+ and E_3 is unstable in the y and z -directions $E_3 \in \Omega(x)$, implies that P lies in R_{ux}^+ . Thus $\Delta(P)$ is E_0 or E_1 or E_2 or $O(P)$ is unbounded and each of them results in a contradiction.

If (H5) holds, then by analogous arguments E_4 does not belong to $\Omega(x)$ and if inequalities (6.8) hold then by arguments given in Theorem 6.4, $E_4 \notin \Omega(x)$. In the same way we can show that E_5 , if it exists, does not lie in $\Omega(x)$.

In case $E_6 \in \Omega(x)$, then as $\xi > 0$, by the Butler- McGehee Lemma and hypotheses (H7) there exists a point P in $\Omega(x) \cap W^s(E_6)$ and the unbounded orbit through P lies in $\Omega(x) \cap R_{uzy}^+$, which is a contradiction. Similarly we get that E_7 and E_8 do not belong to $\Omega(x)$.

Finally no point on the boundary of R_{uzyx}^+ lies in $\Omega(x)$, otherwise $\Omega(x)$ will contain one of the equilibria or closed orbits, resulting in a contradiction. This completes the proof of the theorem.

We now give an example illustrating facultative mutualism between the

mutualist u and the prey x . Consider the system

$$\begin{aligned} u' &= u \left(1 - \frac{u}{L+x} \right), \\ x' &= \alpha x \left(1 - \frac{x}{K} \right) - \gamma_0 xy - \delta_0 xz, \\ y' &= y(-s_{10} - s_{11}u - s_{12}y + \frac{c_1}{1+mu}\gamma_0 x - \delta_1 z), \\ z' &= z(-s_{20} - s_{21}u - s_{22}z + c_2\delta_0 x + (c_{30} + c_{31}u)\delta_1 y). \end{aligned} \quad (6.11)$$

When $L = 3, \alpha = K = 4, \gamma_0 = \delta_0 = 1, s_{10} = \frac{1}{3}, s_{11} = \frac{1}{6}, s_{12} = \frac{1}{4}, c_1 = 3, m = 0, \delta_1 = 1, s_{20} = s_{21} = s_{22} = \frac{1}{3}, c_2 = 1, c_{30} = \frac{1}{3}$ and $c_{31} = 0$, the above system has the boundary equilibria, $E_0(0, 0, 0, 0), E_1(3, 0, 0, 0), E_2(0, 4, 0, 0), E_3(7, 4, 0, 0), E_4(0, \frac{16}{39}, \frac{140}{39}, 0), E_5(0, \frac{5}{4}, 0, \frac{11}{4}), E_6(\frac{63}{16}, \frac{15}{16}, \frac{49}{16}, 0), E_7(\frac{17}{3}, \frac{8}{3}, 0, \frac{4}{3})$ and $E_8(0, \frac{59}{60}, \frac{8}{15}, \frac{149}{60})$.

We now show that for the system (6.11), $E_4(0, x_1, y_1, 0)$ is always globally asymptotically stable in R_{xy}^+ . For this we consider the Lyapunov function

$$V(x, y) = \int_{x_1}^x \frac{(-s_{10} - s_{12}y_1 + c_1\gamma_0\xi)}{\gamma_0\xi} d\xi + y - y_1 - y_1 \ln \frac{y}{y_1},$$

on R_{xy}^+ . Computing the derivative of $V(x, y)$ along the solutions of system (6.11), after some simplifications we get

$$\dot{V} \leq -c_1\alpha(x - x_1)^2 \leq 0.$$

Now as the set $\{(x, y) \in R_{xy}^+ : \dot{V} = 0\} = \{E_4\}$ is invariant we conclude that E_4 is globally asymptotically stable in R_{xy}^+ . Similarly one can see that E_5 is globally asymptotically stable in R_{xy}^+ . Further, as $\beta_1 = \frac{49}{6}, \beta_2 = \frac{4}{3}, \gamma = \frac{149}{117}$ and $\delta = \frac{2}{3}$, all the three-dimensional subsystems are uniformly persistent.

Next we consider the global asymptotic stability of the interior equilibria in the three-dimensional subsystems.

Computing the symmetric matrix $B(u, x, y)$ for $E_6\left(\frac{63}{16}, \frac{15}{16}, \frac{49}{16}, 0\right)$ we get

$$b_{11} = \frac{16}{63}, b_{12} = \frac{-16u}{126(3+x)}, b_{13} = \frac{1}{12},$$

$$b_{22} = 3, b_{23} = 0, b_{33} = \frac{1}{4}.$$

The region of attraction is contained in the set

$$A_1 = \{(u, x, y) \in R_{uxy}^+ : 0 \leq u \leq 7, 0 \leq x \leq 4, 0 \leq y \leq \frac{140}{3}\}.$$

It can be easily verified that the principal minors of $B(u, x, y)$ are positive in A_1 and therefore $B(u, x, y)$ is positive definite in A_1 .

Next the symmetric matrix $D(u, x, z)$ for $E_7\left(\frac{17}{3}, \frac{8}{3}, 0, \frac{4}{3}\right)$ is given by

$$d_{11} = \frac{3}{17}, d_{12} = \frac{3u}{34(3+x)}, d_{13} = \frac{1}{6},$$

$$d_{22} = 1, d_{23} = 0, d_{33} = \frac{1}{3}.$$

The region of attraction for the subsystem in R_{uxz}^+ is contained in the set

$$A_2 = \{(u, x, z) \in R_{uxz}^+ : 0 \leq u \leq 7, 0 \leq x \leq 4, 0 \leq z \leq 11\},$$

and $D(u, x, z)$ is positive definite in A_2 .

For the equilibrium E_8 the matrix $\mathcal{F}(x, y, z)$ is $\text{diag}(1, \frac{1}{9}, \frac{1}{3})$. Finally as $\xi = \frac{15}{48}$ and $\eta = \frac{3}{18}$, from Theorem 6.5 we obtain uniform persistence for the system (6.11).

Finally we demonstrate that uniform persistence can occur even when one or more of the three-dimensional subsystems have almost periodic solutions. We note that the closure Σ of an almost periodic orbit is a compact, minimal set and every solution in Σ is almost periodic (Theorem 2.8).

Suppose the subsystem in R_{uzy}^+ has k non-trivial almost periodic solutions $(\phi_i(t), \psi_i(t), \xi_i(t), 0)$ with disjoint closures Σ_i , $i = 1, 2, \dots, k$. For the subsystems in R_{uzy}^+ and R_{zyx}^+ as before we assume the following:

(H8) Let the equilibria E_7 and E_8 be globally asymptotically stable with respect to solutions starting in R_{uzy}^+ and R_{zyx}^+ , respectively.

THEOREM 6.6. *Let the hypotheses $H(1-6, 8)$, $G(1, 2)$, $P(1, 2)$ and $S(1-3)$ hold. Also let the omega limit sets of all solutions initiating in R_{uzy}^+ lie in the acyclic set $\{\bigcup_{i=1}^k \Sigma_i \cup E_8\}$. Then the system (3.1) is uniformly persistent whenever $\xi > 0$, $\eta > 0$ and*

$$\lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t [-s_2(\phi_i(r), 0) + c_2(\phi_i(r))p_2(\phi_i(r), \psi_i(r)) + c_3(\phi_i(r))q(\phi_i(r), \xi_i(r))] dr > 0, \quad i = 1, \dots, k. \quad (6.12)$$

PROOF: First we observe that from Theorem 2.7, the limit in the inequality (6.12) exists. Also as each Σ_i is a compact minimal set, it lies in R_{uzy}^+ and the subsystem in R_{uzy}^+ is uniformly persistent. The uniform persistence of (3.1) will follow from the Theorem 2.11, if we can show that the stable sets, $W^s(\Sigma_i)$ or $W^s(E_j)$ do not intersect R_{uzyx}^+ and each of them is isolated in $\overline{R_{uzyx}^+}$.

First, we show that $W^s(\Sigma_i) \cap R_{uzyz}^+ = \emptyset$, $1 \leq i \leq k$. Let

$\Phi(t) = (\phi(t), \psi(t), \xi(t), 0)^T$ be any almost periodic solution in Σ_{i_0} and $X(t) = (u(t), x(t), y(t), z(t))^T$, $X(0) = X_0 \in R_{uzyz}^+$ be any solution starting sufficiently close to $\Phi(t)$. Linearizing $X(t)$ about $\Phi(t)$ we obtain

$$Y'(t) = A(t)Y(t), \quad (6.13)$$

where $Y(t) = (u_1(t), x_1(t), y_1(t), z_1(t))^T$ is the linearized vector variable, and

$$A(t) = \begin{pmatrix} \phi h_u + h & \phi h_x & \phi h_y & \phi h_z \\ \alpha \psi g - \psi p_1 & \alpha g + \alpha g_x & -p_1 & -p_2 \\ & -\xi p_{1z} & & \\ -\psi(-s_{1u} + c'_1 p_{1u}) & \psi c_1 p_{1z} & -s_1 + c_1 p_1 & -q \\ & & -\xi s_{1y} & \\ 0 & 0 & 0 & -s_2 + c_2 p_2 + c_3 q \end{pmatrix},$$

where all the functions are evaluated at $\Phi(t)$. Solving the last equation in (6.13) we obtain

$$z_1(t) = z_1(0) \exp \int_0^t [-s_2(\phi(r), 0) + c_2(\phi(r)) p_2(\phi(r), \psi(r)) + c_3(\phi(r)) q(\phi(r), \xi(r))] dr.$$

Now since $\Phi(t)$ lies in Σ_{i_0} and the solutions through Σ_{i_0} are uniformly stable in both directions in Σ_{i_0} , the inequality (6.12) (with $i = i_0$) implies that $z_1(t) > 0$ for $t \geq 0$ and is an increasing function for sufficiently large t . Thus any solution in R_{uzyz}^+ , starting sufficiently close to Σ_{i_0} eventually gets away from it.

Hence, $\Omega(x_0) \not\subset \Sigma_{i_0}$. Thus $W^s(\Sigma_{i_0}) \cap R_{uzyz}^+ = \emptyset$, $1 \leq i \leq k$.

Since all boundary equilibria are hyperbolic we conclude that $W^s(E_i) \cap$

$$R_{uzyz}^+ = \emptyset, 1 \leq i \leq 8.$$

Now suppose that for some i_0 , Σ_{i_0} is not an isolated invariant set in R_{uxyz}^+ . Then there must exist closed invariant sets in arbitrarily close neighbourhoods of Σ_{i_0} . Let $M \supset \Sigma_{i_0}$ be such a closed invariant set. Then by repeating the arguments, given above we conclude that Σ_{i_0} repels the solutions starting in M/Σ_{i_0} and hence they must leave M . However this contradicts the fact that M is invariant. Hence the proof.

Remark 6.3 The acyclic condition of the above theorem is always satisfied when each Σ_i is either asymptotically stable or completely unstable in R_{uxy}^+ and there do not exist any homoclinic orbits in R_{uxy}^+ .

Remark 6.4 In the event that almost periodic solutions exist for the subsystems in R_{uxx}^+ and/or R_{xyz}^+ , a criterion similar to the one given by the above theorem can be obtained. In case of the food chain in R_{xyz}^+ the mean value integral condition is automatically satisfied as $h(0, x, y, z)$ is always positive.

6.3 Extinction

Here we obtain extinction results for the three-dimensional subsystems and the system (3.1).

With $\tilde{M}, \tilde{N}$ and $\tilde{K}$ as in (3.3), define

$$L_1 = L(0, \tilde{M}, 0) \text{ and } L_2 = L(0, 0, \tilde{N}). \quad (6.14)$$

THEOREM 6.7. Let hypotheses $H(1-4)$, $G(1,2)$, $P(1,2)$ and $S(1-3)$ hold. If

$$-s_1(L_1, 0) + c_1(L_1)p_1(L_1, \tilde{K}) < 0, \quad (6.15)$$

then $\mathcal{E}_{y \rightarrow 0}$ in R_{uzy}^+ .

PROOF: See Freedman and Rai (1987a).

Similarly one can show that the following result holds for the predator-prey-mutualist system in R_{uxz}^+ .

THEOREM 6.8. Let hypotheses $H(1-4)$, $G(1,2)$, $P(1,2)$ and $S(1,2)$ hold. Whenever

$$-\tilde{s}_2 + c_2(L_2)p_2(L_2, \tilde{K}) < 0, \quad (6.16)$$

where $\tilde{s}_2 = \min_{L_2 \leq u \leq \tilde{L}} s_2(u, 0)$ and L_2 is given by (6.14), $\mathcal{E}_{x \rightarrow 0}$ in R_{uxz}^+ .

The following result holds for the food chain.

THEOREM 6.9. Let hypotheses $G(1,2)$, $P(1,2)$ and $S(1-3)$ hold. If

$$-s_2(0, 0) + c_2(0)p_2(0, K(0)) + c_3(0)q(0, M) < 0, \quad (6.17)$$

where M is given by (5.9), then $\mathcal{E}_{x \rightarrow 0}$ in R_{zyx}^+ .

PROOF: $z' = z[-s_2(0, z) + c_2(0)p_2(0, x) + c_3(0)q(0, y)]$
 $\leq z[-s_2(0, 0) + c_2(0)p_2(0, K(0)) + c_3(0)q(0, M)]$. Hence from inequality (6.17),
 $\lim_{t \rightarrow \infty} z(t) = 0$.

Now we obtain extinction results for the system (3.1).

THEOREM 6.10. *Let hypotheses $H(1-4)$, $G(1,2)$, $P(1,2)$ and $S(1-3)$ hold.*

Further let

$$-\tilde{s}_2 + c_2(L_3)p_2(L_3, \tilde{K}) + \tilde{c}_3\tilde{q} < 0, \quad (6.18)$$

where

$$\begin{aligned} L_3 = L(0, \tilde{M}, \tilde{N}), \tilde{s}_2 &= \min_{L_3 \leq u \leq \tilde{L}} s_2(u, 0), \\ \tilde{c}_3 &= \max_{L_3 \leq u \leq \tilde{L}} c_3(u), \tilde{q} = \max_{L_3 \leq u \leq \tilde{L}} q(u, \tilde{M}), \end{aligned} \quad (6.19)$$

$\tilde{L}$ and $\tilde{M}$ are given by (3.3). Then $\mathcal{E}_{x \rightarrow 0}$ in R_{uxyz}^+ .

PROOF: It can be easily seen that $L_3 \leq u(t) \leq \tilde{L}$, for sufficiently large t . This, together with inequality (6.18) yield that $z' < 0$ for large t . Thus

$$\lim_{t \rightarrow \infty} z(t) = 0.$$

Similarly we can prove the following:

THEOREM 6.11. *Let hypotheses $H(1-4)$, $G(1,2)$, $P(1,2)$ and $S(1-3)$ hold. If*

$$-s_1(L_3, 0) + c_1(L_3)p_1(L_3, \tilde{K}) < 0, \quad (6.20)$$

then $\mathcal{E}_{y \rightarrow 0}$ in R_{uxyz}^+ . If in addition

$$-\tilde{s}_2 + c_2(L_3)p_2(L_3, \tilde{K}) < 0,$$

where L_3 and $\tilde{s}_2$ are given by (6.19), then $\mathcal{E}_{yz \rightarrow 0}$ in R_{uzyz}^+ .

6.4 Reversal of Outcome.

We now obtain criteria for uniform persistence of the system (3.1) when one or more of its three-dimensional subsystems exhibit extinction. However, we observe that if the subsystem R_{uzy}^+ becomes extinct, the system (3.1) will eventually reduce to a predator-prey-mutualist system and the Theorems 6.1-6.4 will be applicable.

First we consider the case when the subsystem in R_{uzy}^+ exhibits extinction. For this we assume the following hypotheses:

- (H9) Let the equilibria E_6 and E_8 be globally asymptotically stable in R_{uzy}^+ and R_{zyz}^+ , respectively.

THEOREM 6.12. *Let hypotheses $H(1-6,9)$, $G(1,2)$, $P(1,2)$, $S(1-3)$ and inequality (6.16) hold. If $\xi > 0$, then $\mathcal{E}_{z \rightarrow 0}$ in R_{uzyz}^+ , but the system (3.1) is uniformly persistent.*

PROOF: It follows from Theorem 6.8 that $\mathcal{E}_{z \rightarrow 0}$ in R_{uzyz}^+ . Hence from Theorem 4.8, there does not exist any equilibrium in R_{uzyz}^+ . For $X \in R_{uzyz}^+$, let $\Omega(x)$ denote its omega limit set. Repeating the arguments of Theorem 6.5 we get that $\Omega(x) \cap \{\bigcup_{i=0}^5 E_i\} = \emptyset$. Further $\Omega(x) \cap R_{uzyz}^+ = \emptyset$ for, if there exists a point P in $\Omega(x) \cap R_{uzyz}^+$ then $\Omega(P) = E_3 \in \Omega(x)$, which is a contradiction. The rest of the proof is the same as in Theorem 6.5.

Remark 6.5 We note that the subsystem in R_{uzz}^+ always exhibits extinction in the case of a simple food chain in R_{zyx}^+ .

To illustrate the above theorem we consider system (6.11) with $L = 1, \alpha = \frac{7}{10}, K = 1, \gamma_0 = \frac{7}{10}, \delta_0 = \frac{7}{20}, s_{10} = \frac{1}{4}, s_{11} = 0, s_{12} = \frac{1}{4}, c_1 = 1, m = 0, \delta_1 = \frac{13}{27}, s_{20} = s_{21} = s_{22} = \frac{1}{3}, c_2 = 1, c_{30} = 3$ and $c_{31} = 0$. Here the presence of the mutualist increases the death rate of the top-predator. The boundary equilibria are $E_0(0, 0, 0, 0), E_1(1, 0, 0, 0), E_2(0, 1, 0, 0), E_3(2, 1, 0, 0), E_4(0, \frac{10}{19}, \frac{9}{19}, 0), E_5(0, \frac{30}{41}, 0, \frac{22}{41}), E_6(\frac{29}{19}, \frac{10}{19}, \frac{9}{19}, 0)$ and $E_8(0, \frac{35290}{63859}, \frac{24861}{63859}, \frac{6156}{63859})$.

Since $\beta_1 = \frac{9}{20} > 0$, the predator-prey-mutualist subsystem in R_{uzy}^+ is uniformly persistent. Also as $L_2 = 1$ and $\bar{L} = 2$, the left hand side of inequality (6.14) is equal to $-\frac{19}{60}$ and (6.14) holds. Thus from Theorem 6.12 the subsystem in R_{uzz}^+ exhibits extinction. Further $\gamma = \frac{61}{114} > 0$ and $\delta = \frac{17}{4428} > 0$ imply that the food chain is uniformly persistent.

The symmetric matrix corresponding to E_6 is $\text{diag}(\frac{19}{29}, \frac{7}{10}, \frac{1}{4})$. Thus E_6 is globally asymptotically stable with respect to solutions in R_{uzy}^+ . The symmetric matrix $\mathcal{F}(x, yz)$ for E_8 is given by $d_{11} = \frac{7}{10}, d_{12} = -\frac{7}{10}, d_{13} = 0, d_{22} = \frac{3}{4}, d_{23} = 0$ and $d_{33} = 13$, which is also positive definite. Finally, $\xi = \frac{3}{114} > 0$ implies that the system is uniformly persistent.

Now we consider the case when the food chain in R_{zyx}^+ becomes extinct.

For this we assume the following:

(H10) Let E_6 and E_7 be globally asymptotically stable with respect to solutions initiating in R_{uzy}^+ and R_{uzz}^+ , respectively.

THEOREM 6.13. Let the hypotheses $H(1-5, 10), G(1, 2), P(1, 2), S(1-3)$ and inequality (6.17) hold. If $\xi > 0$ and $\eta > 0$ then $\mathcal{E}_{s \rightarrow 0}$ in R_{xyz}^+ but the system (3.1) is uniformly persistent.

PROOF: From Theorem 6.9 it follows that the food chain exhibits extinction. Since $\alpha_1 < 0$, from Theorem 4.4 we get that E_5 does not exist. Also from Theorem 4.8, E_8 does not exist. Uniform persistence for the system follows by arguments similar to those for Theorem 6.12.

To illustrate the above theorem we consider system (6.11) with $\alpha = L = K = 1, \gamma_0 = \frac{2}{3}, \delta_0 = \frac{1}{10}, s_{10} = s_{12} = \frac{1}{3}, s_{11} = 0, c_1 = 1, m = 0, \delta_1 = \frac{1}{6}, s_{20} = \frac{2}{5}, s_{21} = -\frac{1}{5}, s_{22} = \frac{1}{5}, c_2 = 2$ and $c_3 = \frac{1}{10}$. Here the mutualist provides the top-predator with alternate food supply.

The boundary equilibria are $E_0(0, 0, 0, 0), E_1(1, 0, 0, 0), E_2(0, 1, 0, 0), E_3(2, 1, 0, 0), E_4(0, \frac{5}{7}, \frac{3}{7}, 0), E_6(\frac{12}{7}, \frac{5}{7}, \frac{3}{7}, 0)$ and $E_7(\frac{23}{12}, \frac{11}{12}, 0, \frac{10}{12})$.

The region of attraction is contained in the set

$$\mathcal{A} = \{(u, x, y, z) \in \bar{R}_{uxyz}^+ : 0 \leq u \leq 2, 0 \leq x \leq 1, 0 \leq y \leq 1, 0 \leq z \leq \frac{13}{12}\}.$$

It is easily seen that the inequality (6.17) holds and therefore the food chain becomes extinct. However, as $\beta_1 = \frac{1}{3}$ and $\beta_2 = \frac{2}{5}$, the subsystems in R_{uzy}^+ and R_{uwx}^+ are uniformly persistent.

The symmetric matrix $B(u, x, y)$ corresponding to E_6 is given by $b_{11} = \frac{7}{12}, b_{12} = -\frac{7u}{24(1+z)}, b_{13} = 0, b_{22} = 1, b_{23} = 0$ and $b_{33} = \frac{1}{3}$. Also, $B(u, x, y)$ is

positive definite in the region of attraction contained in

$$A_1 = \{(u, x, y) \in \bar{R}_{uxy}^+ : 0 \leq u \leq 2, 0 \leq x \leq 1, 0 \leq y \leq 1\}.$$

Thus E_6 is globally stable in R_{uxx}^+ . Further the symmetric matrix $D(u, x, z)$ corresponding to E_7 is given by $d_{11} = \frac{12}{23}$, $d_{12} = -\frac{6u}{23(1+x)}$, $d_{13} = -\frac{1}{10}$, $d_{22} = 2$, $d_{23} = 0$ and $d_{33} = \frac{1}{5}$. Again $D(u, x, z)$ is positive definite in the region of attraction contained in the set

$$A_2 = \{(u, x, z) \in \bar{R}_{uxz}^+ : 0 \leq u \leq 2, 0 \leq x \leq 1, 0 \leq z \leq 1\}.$$

Further, as $\xi = \frac{13}{140}$ and $\eta = \frac{5}{36}$ we conclude that the system is uniformly persistent.

Finally we consider the case when the subsystems in R_{uxx}^+ and R_{zyx}^+ , both become extinct.

THEOREM 6.14. *Let hypotheses $H(1-5)$, $G(1,2)$, $P(1,2)$, $S(1-3)$ and inequalities (6.16) and (6.17) hold. Further let E_6 be globally asymptotically stable in R_{uxy}^+ and $\xi > 0$. Then $\mathcal{E}_{x \rightarrow 0}$ both in R_{uxx}^+ and R_{zyx}^+ but the system (3.1) is uniformly persistent.*

PROOF: The extinction of the subsystems in R_{uxx}^+ and R_{zyx}^+ follows from Theorems 6.8 and 6.9. Since $\alpha_1 < 0$, from Theorem 4.4 equilibrium E_5 does not exist. Also Theorem 4.8 implies that E_7 and E_8 do not exist. Uniform persistence of (3.1) follows by arguments similar to those for Theorem 6.12.

As an example we consider the system (6.11) with $L = 1, \alpha = K = 2, \gamma_0 = \frac{1}{4}, \delta_0 = \frac{1}{6}, s_{10} = s_{12} = \frac{1}{4}, s_{11} = 0, c_1 = 1, m = \frac{1}{9}, \delta_1 = 1, s_{20} = s_{22} = \frac{1}{3}, s_{21} = 0, c_2 = \frac{1}{4}$ and $c_{30} = c_{31} = \frac{1}{10}$. Here the mutualist decreases the predator response of the predator y and increases the rate of conversion of prey biomass to predator bio-mass for the top-predator z .

The region of attraction is contained in the set

$$A = \{(u, x, y, z) \in \bar{R}_{uzyx}^+ : 0 \leq u \leq 3, 0 \leq x \leq 2, 0 \leq y \leq 1, 0 \leq z \leq \frac{9}{20}\}.$$

The boundary equilibria are $E_0(0, 0, 0, 0), E_1(1, 0, 0, 0), E_2(0, 2, 0, 0), E_3(3, 2, 0, 0), E_4(0, \frac{5}{4}, \frac{2}{3}, 0)$ and $E_6(5+\sqrt{61}, -6+\sqrt{61}, 10-\sqrt{61}, 0)$. The subsystems in R_{uzy}^+ and R_{xyz}^+ satisfy inequalities (6.16) and (6.17), respectively and therefore exhibit extinction. But the subsystem in R_{uzy}^+ is uniformly persistent, as $\beta = \frac{1}{8} > 0$.

The symmetric matrix $B(u, x, y)$ corresponding to E_6 is given by $b_{11} = \frac{1}{5+\sqrt{61}}, b_{12} = -\frac{u}{2(5+\sqrt{61})(1+x)}, b_{13} = 0, b_{22} = 1, b_{23} = 0$ and $b_{33} = \frac{1}{4}$. Further $B(u, x, y)$ is positive definite in its region of attraction A_1 , where

$$A_1 = \{(u, x, y) \in \bar{R}_{uzy}^+ : 0 \leq u \leq 3, 0 \leq x \leq 2, 0 \leq y \leq 1\}.$$

Finally since $\xi \approx 2.8$, we conclude that the system is uniformly persistent.

Remark 6.6 All of the above results can be improved by allowing the possibility of periodic or almost periodic solutions for the subsystems of the system (3.1), as shown in §6.1.

The preceding results demonstrate that the system (3.1) can be uniformly persistent even when one or more of its three-dimensional subsystems exhibit extinction. In particular Theorems 6.13 and 6.14 show that the action of a mutualist can result in the long term survival of a food chain which would otherwise become extinct. However a mutualist can also make a uniformly persistent food chain exhibit extinction. We illustrate this with the help of the following example, where the presence of the mutualist increases the death rate of the predators.

Consider the system

$$\begin{aligned} u' &= u(1 - \frac{u}{1+x}), \\ x' &= x(3-x) - xy - xz, \\ y' &= y(-\frac{5}{18}(1+u+y) + \frac{5}{9}x) - \frac{yz}{y+1}, \\ z' &= z(-\frac{1}{2} - \frac{3}{5} - u - \frac{1}{10}z + \frac{1}{6}x + \frac{1}{2}\frac{y}{y+1}). \end{aligned} \quad (6.21)$$

Its boundary equilibria are $E_0(0,0,0,0)$, $E_1(1,0,0,0)$, $E_2(0,3,0,0)$, $E_3(4,3,0,0)$, $E_4(0, \frac{4}{3}, \frac{5}{3}, 0)$, $E_5(\frac{7}{2}, \frac{5}{2}, \frac{1}{2}, 0)$ and $E_6(0, \frac{5a^2-8a+59}{10a+28}, a, \frac{-15a^2+10+25}{10a+28})$, where $a^3 = \frac{20}{7}$.

The region of attraction is contained in the set,

$$A = \{(u, x, y, z) \in R_{uxyz}^+ : 0 \leq u \leq 4, 0 \leq x \leq 3, 0 \leq y \leq 5, 0 \leq z \leq 5\}.$$

Since $\beta_1 = \frac{5}{18}$, the subsystem in R_{uxy}^+ is uniformly persistent. Further as E_5 does not exist and $\gamma = \frac{5}{144}$, the food chain is also uniformly persistent. However the system (6.21) satisfies inequality (6.18) and therefore the top-predator will eventually become extinct.

CHAPTER 7

MUTUALISM WITH HIGHER TROPHIC LEVELS

7.1 Preliminaries

This chapter deals with the interactions of the mutualist with the second and third trophic levels. Specifically we consider the cases of facultative and obligate interactions between the mutualist u and the predator y and obligate mutualism between u and the predator z . We note that in all the three cases (3.1) represents a dissipative system (see Theorems 3.2 and 3.3). In the following sections the numbers $\alpha_1, \beta_1, \beta_2, \gamma, \delta, \xi$ and η denote the various eigenvalues, as defined in §6.1. We will also make use of the hypotheses $H(5 - 10)$ introduced in the previous chapter.

7.2 Uniform Persistence

Case I

The system (3.1) exhibits facultative mutualism with the predator y when the hypotheses $H(1, 2, 3', 4')$, $G(1, 2, 3')$, $P(1, 2')$, and $S(1, 2', 3')$, as described in §3.3 hold.

The set $\mathcal{B}$, given by Theorem 3.2 contains the region of attraction for (3.1). The criteria for the existence of boundary equilibria and for uniform persistence remain the same as in Chapter 6. In particular the following result holds:

THEOREM 7.1. *Let hypotheses $H(1, 2, 3', 4', 5-7)$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2', 3)$ hold. Then the system (3.1) is uniformly persistent whenever $\xi > 0$ and $\eta > 0$.*

The proof is similar to the one given for Theorem 6.5.

The above theorem describes the circumstances in which the mutualistic interaction between u and y does not dominate the interactions of the food chain and all the species can coexist. We will illustrate the various ways in which mutualism between the mutualist u and predator y can occur in Case II below. Here we give an example in which the mutualist u provides the predator y with an alternate food supply and increases the death rate of the top-predator.

Consider the system

$$\begin{aligned} u' &= u \left(1 - \frac{u}{L + \ell y} \right), \\ x' &= \alpha x \left(1 - \frac{x}{K + ku} \right) - (\gamma_0 + \gamma_1 u)xy - \frac{\delta_0}{1 + \delta_1 u}xz, \\ y' &= y(-s_{10} + s_{11}u - s_{12}y + (c_{10} + c_{11}u)(\gamma_0 + \gamma_1 u)x - \xi_0 z), \\ z' &= z(-s_{20} - s_{21}u - s_{22}z + \frac{c_{20}}{1 + c_{21}u} \frac{\delta_0}{1 + \delta_1 u}x + \frac{c_{30}\xi_0}{1 + c_{31}u}y), \end{aligned} \quad (7.1)$$

where all the constants are assumed to be nonnegative. With $L = 1$, $\ell = \frac{1}{3}$, $\alpha = K = 3$, $\gamma_0 = \delta_0 = 1$, $k = \gamma_1 = \delta_1 = c_{11} = c_{21} = c_{31} = 0$, $s_{10} = s_{12} = \frac{1}{3}$, $s_{11} = \frac{1}{4}$, $c_{10} = \frac{1}{4}$, $s_{20} = 1$, $s_{21} = \frac{1}{3}$, $s_{22} = \frac{1}{2}$, $c_{20} = \frac{7}{8}$, $\xi_0 = \frac{1}{38}$, $c_{30} = 4$, the boundary equilibria are $E_0(0, 0, 0, 0)$, $E_1(1, 0, 0, 0)$, $E_2(0, 3, 0, 0)$, $E_3(1, 3, 0, 0)$, $E_4(0, \frac{16}{7}, \frac{5}{7}, 0, 0)$, $E_5(0, \frac{20}{11}, 0, \frac{13}{11})$, $E_6(\frac{52}{41}, \frac{90}{41}, \frac{33}{41}, 0)$, $E_7(1, \frac{20}{11}, 0, \frac{13}{11})$ and $E_8(0, \frac{2640}{1529}, \frac{315}{1529}, \frac{1632}{1529})$.

The region of attraction is contained in the set

$$B = \{(u, x, y, z) : 0 \leq u \leq \frac{34}{23}, 0 \leq x \leq 3, 0 \leq y \leq \frac{33}{23}, 0 \leq z \leq \frac{985}{276}\}.$$

Since $\beta_1 = \frac{11}{24}$, $\beta_2 = \frac{41}{24}$, $\gamma = \frac{68}{23}$, $\delta = \frac{35}{396}$, we conclude that all of the three dimensional subsystems are uniformly persistent.

The symmetric matrix $\mathcal{B}(u, x, y)$ corresponding to E_6 is given by, $b_{11} = \frac{41}{52}$, $b_{12} = 0$, $b_{13} = -\frac{1}{2} \left(\frac{41u}{156(1+\frac{1}{3}y)} + \frac{1}{24} \right)$, $b_{22} = \frac{1}{4}$, $b_{23} = 0$ and $b_{33} = \frac{1}{3}$. Further it is positive definite in the region of attraction

$$B_1 = \{(u, x, y, z) : 0 \leq u \leq \frac{34}{23}, 0 \leq x \leq 3, 0 \leq y \leq \frac{33}{23}\}.$$

The symmetric matrix $\mathcal{D}(u, x, z)$ corresponding to E_7 is given by, $d_{11} = 1$, $d_{12} = 0$, $d_{13} = \frac{1}{6}$, $d_{22} = \frac{7}{8}$, $d_{23} = 0$ and $d_{33} = \frac{1}{2}$. Also the matrix $\mathcal{F}(x, y, z)$, corresponding to E_8 is given by $f_{11} = 1$, $f_{12} = 0$, $f_{13} = \frac{1}{16}$, $f_{22} = \frac{4}{3}$, $f_{23} = 0$ and $f_{33} = \frac{1}{2}$. Since the principal minors of $\mathcal{D}(u, x, z)$ and $\mathcal{F}(x, y, z)$ are positive we conclude that E_7 and E_8 are also globally asymptotically stable in $R_{u,x,z}^+$ and $R_{x,y,z}^+$ respectively.

Finally $\xi = \frac{281}{492}$ and $\eta = \frac{103}{792}$ imply that the system (7.1) is uniformly persistent. The interior equilibrium is $E^* \left(\frac{3268}{2799}, \frac{584}{311}, \frac{469}{933}, \frac{578}{933} \right)$.

Case II

The mutualism between the mutualist u and predator y is obligate whenever the hypothesis (S3) of Case I is violated. Thus we suppose that (3.1) satisfies the hypotheses $H(1, 2, 3', 4')$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2, 3')$. The obligate relationship implies that $\mathcal{E}_{y \rightarrow 0}$ in R_{xy}^+ and R_{xyz}^+ . Thus the equilibria E_4 and E_8 do not exist. The subsystems in R_{uzy}^+ and $R_{u,x,z}^+$ can however be uniformly persistent.

THEOREM 7.2. *Let the hypotheses $H(1, 2, 3', 4')$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2, 3')$ hold. Then the subsystem in R_{uzy}^+ is uniformly persistent whenever $\beta_1 > 0$.*

The proof can be found in Freedman et al. (1987b). The following result can be obtained in a similar way.

THEOREM 7.3. *Let the hypotheses $H(1, 2, 3', 4', 6)$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2, 3')$ hold. Then the subsystem in R_{uzy}^+ is uniformly persistent whenever $\beta_2 > 0$.*

The following result gives a criterion for uniform persistence of the system (3.1).

THEOREM 7.4. *Let the hypotheses $H(1, 2, 3', 4', 6, 10)$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2, 3')$ hold. Then the subsystem in (3.1) is uniformly persistent whenever $\xi > 0$ and $\eta > 0$.*

The proof is similar to the proof of Theorem 6.13.

Theorem 7.4 can be interpreted biologically as follows. If the predator y is unable to survive on its own, then mutualist could help the predator population to survive. As observed by Freedman et al. (1987b) the mutualist can benefit the mutualist-predator in several ways: by increasing the prey growth rate, by increasing the rate of predation of its prey x , by providing an alternate food source for the mutualist-predator and by enhancing the efficiency of utilization

of the prey by the mutualist-predator. Next we illustrate each of these cases with an example. All the examples considered are given by (7.1).

In the absence of the mutualist u , there will be an equilibrium in R_{xy}^+ ,

$$(x, y) = \left(\frac{K(s_{10}\gamma_0 + \alpha s_{12})}{\alpha s_{12} + Kc_{10}\gamma_0^2}, \frac{\alpha(Kc_{10}\gamma_0 - s_{10})}{\alpha s_{12} + Kc_{10}\gamma_0^2} \right),$$

unless $Kc_{10}\gamma_0 \leq s_{10}$. Thus for obligate mutualism we require

$$Kc_{10}\gamma_0 \leq s_{10}. \quad (7.2)$$

Example 1 When $\gamma_1 = \delta_1 = s_{11} = c_{11} = s_{21} = c_{21} = c_{31} = 0$ and $k > 0$, mutualism occurs by means of the mutualist enhancing the prey growth rate.

The region of attraction for the system is contained in the set

$$B = \{(u, x, y, z) : 0 \leq u \leq L + \ell\tilde{M}, 0 \leq x \leq K + k(L + \ell\tilde{M}), 0 \leq y \leq \tilde{M}, 0 \leq z \leq \tilde{N}\}, \quad (7.3)$$

where

$$\tilde{M} = \frac{-s_{10} + c_{10}\gamma_0(K + kL)}{s_{12} - c_{10}\gamma_0 k\ell} \text{ and } \tilde{N} = \frac{1}{s_{22}}(-s_{20} + Kc_{20}\delta_0 + K(L + \ell\tilde{M}) + c_{30}\xi_0\tilde{M}).$$

We assume that $\tilde{M}$ and $\tilde{N}$ are positive, otherwise the system will always exhibit extinction. The equilibria in $\overline{R_{ux}^+}$ are $E_0(0, 0, 0, 0)$, $E_1(L, 0, 0, 0)$, $E_2(0, K, 0, 0)$, $E_3(L, K + kL, 0, 0, 0)$. The equilibrium $E_5\left(0, \frac{K(\delta_0 s_{20} + \alpha s_{22})}{\alpha s_{22} + Kc_{20}\delta_0^2}, 0, \frac{\alpha(-s_{20} + Kc_{20}\delta_0)}{\alpha s_{22} + Kc_{20}\delta_0^2}\right)$ exists provided $Kc_{20}\delta_0 > s_{20}$.

The subsystem in R_{uxy}^+ is uniformly persistent whenever

$$\beta_1 = -s_{10} + c_{10}\gamma_0(K + kL) > 0, \quad (7.4)$$

in which case the equilibrium in R_{usz}^+ is given by $E_6(u_3, x_3, y_3, 0)$

$= (L + \ell y_3, \frac{s_{10} + s_{12} y_3}{c_{10} \gamma_0}, y_3, 0)$ where

$$y_3 = \frac{b + \sqrt{b^2 + 4k\ell c_{10} \gamma_0^2 \beta_1}}{2k\ell c_{10} \gamma_0^2}$$

and

$$b = \alpha k \ell c_{10} \gamma_0 - \alpha s_{12} - c_{10} \gamma_0^2 (K + kL).$$

The subsystem in R_{usz}^+ is uniformly persistent provided

$$\beta_2 = -s_{20} + c_{20} \delta_0 (K + kL) > 0, \quad (7.5)$$

and then the equilibrium in R_{usz}^+ is given by

$$E_7(u_4, x_4, 0, z_4) = (L, \frac{(\alpha s_{22} + \delta_0, s_{20})(K + kL)}{\alpha s_{22} + (K + kL)c_{20} \delta_0^2}, 0, \frac{\alpha \beta_2}{\alpha s_{22} + (K + kL)c_{20} \delta_0^2}).$$

The symmetric matrix $\mathcal{B}(u, x, y)$ corresponding to E_6 is given by $b_{11} = \frac{1}{(L + \ell y_3)}$,

$$b_{12} = \frac{-\alpha k c_{10} z}{2(K + ku)(K + k(L + \ell y_3))}, b_{13} = -\frac{\ell u}{2(L + \ell y)(L + \ell y_3)}, b_{22} = \frac{\beta c_{10}}{K + k(L + \ell y_3)}, b_{23} = 0$$

and $b_{33} = s_{12}$. It is positive definite in the region of attraction of the subsystem in R_{usz}^+ , whenever

$$s_{12} \left(\frac{\alpha c_{10}}{L + \ell y_3} - \frac{\alpha^2 k^2 c_{10}^2 (K + k(L + \ell \bar{M}))^2}{4K^2 (K + k(L + \ell y_3))} \right) - \frac{\alpha c_{10} \ell^2 (L + \ell \bar{M})^2}{4L^2 (L + \ell y_3)^2} > 0. \quad (7.6)$$

The matrix $\mathcal{D}(u, x, z)$ corresponding to E_7 is given by $d_{11} = \frac{1}{L}$, $d_{12} = \frac{\alpha k c_{20} z}{2(K + kL)(K + ku)}$,

$d_{13} = 0$, $d_{22} = \frac{\alpha c_{20}}{K + kL}$, $d_{23} = 0$, $d_{33} = s_{22}$. It is positive definite whenever

$$\frac{1}{L} - \frac{\alpha k^2 c_{20} (K + kL)^2}{4(K + kL)K^2} > 0. \quad (7.7)$$

Thus the system (7.1) will be uniformly persistent whenever (7.4)-(7.7) hold and

$$\xi = -s_{20} + c_{20}\delta_0 x_3 + c_{30}\xi_0 y_3 > 0, \quad (7.8)$$

and

$$\eta = -s_{10} + c_{10}\gamma_0 x_4 - \xi_0 z_4 > 0. \quad (7.9)$$

Example 2 When $k = \delta_1 = s_{11} = c_{11} = s_{21} = c_{21} = c_{31} = 0$ and $\gamma_1 > 0$, the mutualist enhances the rate of predation of the mutualist-predator y . Here the region of attraction is contained in the set

$$\begin{aligned} B = \{ (u, x, y, z) : 0 \leq u \leq L + \ell \tilde{M}, 0 \leq x \leq K, 0 \leq y \leq \tilde{M}, \\ 0 \leq z \leq \frac{1}{s_{22}} (-s_{20} + Kc_{20}\delta_0 + c_{30}\xi_0 \tilde{M}), \end{aligned} \quad (7.10)$$

where

$$\tilde{M} = -\frac{s_{10} + Kc_{10}(\gamma_0 + \gamma_1 L)}{s_{12} - Kc_{10}\gamma_1 \ell}.$$

The equilibrium in $\overline{R_{ux}^+}$ are given by $E_0(0, 0, 0, 0)$, $E_1(L, 0, 0, 0)$, $E_2(0, K, 0, 0)$ and $E_3(L, K, 0, 0)$.

The subsystem in R_{uzy}^+ is uniformly persistent whenever

$$\beta_1 = -s_{10} + Kc_{10}(\gamma_0 + \gamma_1 L) > 0. \quad (7.11)$$

In which case the equilibrium $E_6(u_3, x_3, y_3, 0) = (L + \ell y_3, \frac{1}{\alpha}[\alpha - (\gamma_0 + \gamma_1(L + \ell y_3))y_3], y_3, 0)$, where from Descartes' rule of signs y_3 is the unique positive root of the equation

$$y^3 + \frac{2}{\gamma_1 \ell}(\gamma_0 + \gamma_1 L)y^2 + (Kc_{10}(\gamma_0 + \gamma_1 L)^2 + \alpha s_{12} - \alpha Kc_{10}\gamma_1 \ell)y - \alpha \beta_1 = 0. \quad (7.12)$$

The subsystem in $R_{u_{zx}}^+$ is uniformly persistent provided

$$\beta_2 = -s_{20} + c_{20} \delta_0 K > 0, \quad (7.13)$$

in which case $E_7(u_4, x_4, 0, z_4) = \left(L, \frac{K(\alpha s_{22} + \delta_0 s_{20})}{\alpha s_{22} + K c_{20} \delta_0^2}, 0, \frac{\alpha \beta_2}{\alpha s_{22} + K c_{20} \delta_0^2} \right)$. Now we consider the global asymptotic stability of E_6 and E_7 in $R_{u_{zy}}^+$ and $R_{u_{zx}}^+$, respectively.

The symmetric matrix $B(u, x, y)$ corresponding to $E_6(u_3, x_3, y_3, 0)$ is given by $b_{11} = \frac{1}{u_3}$, $b_{12} = \frac{\gamma_1 y}{2}$, $b_{13} = -\frac{1}{2} \left(\frac{\ell u}{u_3(L + \ell y)} + c_{10} \gamma_1 x - s_{11} \right)$, $b_{22} = \frac{c_{10}}{K}$, $b_{23} = 0$ and $b_{33} = s_{12}$. It is positive definite in its region of attraction whenever

$$\frac{4}{s_{12}} \left(\frac{1}{K u_3} - \frac{\gamma_1^2 c_{10} \tilde{M}^2}{4} \right) - \frac{1}{K} \left(\frac{\ell(L + \ell \tilde{M})}{u_3 L} + K c_{10} \gamma_1 - s_{11} \right) > 0, \quad (7.14)$$

where $\tilde{M}$ is given by (7.10). The symmetric matrix $D(u, x, z)$ corresponding to E_7 is given by $d_{11} = \frac{1}{u_4}$, $d_{12} = 0$, $d_{13} = \frac{1}{2} s_{21}$, $d_{22} = \frac{\alpha c_{20}}{K}$, $d_{23} = 0$ and $d_{33} = s_{22}$.

It is positive definite in its region of attraction whenever

$$4s_{22} - L s_{21}^2 > 0. \quad (7.15)$$

Thus whenever (7.11), (7.13)-(7.15) hold and

$$\xi = -s_{20} + c_{20} \delta_0 x_3 + c_3 \xi_0 y_3 > 0, \quad (7.16)$$

and

$$\eta = -s_{10} + c_{10}(\gamma_0 + \gamma_1 u_4)x_4 - \xi_0 z_4 > 0, \quad (7.17)$$

the system (7.1) is uniformly persistent.

Example 3 When $k = \gamma_1 = \delta_1 = c_{11} = s_{21} = c_{21} = c_{31} = 0$ and $s_{11} > 0$, the mutualist provides the mutualist-predator with an alternate food source.

The region of attraction is contained in the set

$$\mathcal{B} = \{(u, x, y, z) : 0 \leq u \leq L + \ell \tilde{M}, 0 \leq x \leq K, 0 \leq y \leq \tilde{M}, 0 \leq z \leq \tilde{N}\}, \quad (7.18)$$

where

$$\tilde{M} = -\frac{s_{10} + s_{11}L + c_{10}\gamma_0 K}{s_{12} - s_{11}\ell} \quad \text{and} \quad \tilde{N} = \frac{1}{s_{22}}(-s_{20} + Kc_{20}\delta_0 + c_3\xi_0\tilde{M}). \quad (7.19)$$

The equilibria in $\overline{R_{ux}^+}$ are $E_0(0, 0, 0, 0)$, $E_1(L, 0, 0, 0)$, $E_2(0, K, 0, 0)$ and $E_3(L, K, 0, 0)$.

The subsystem in R_{uxy}^+ is uniformly persistent whenever

$$\beta_1 = -s_{10} + s_{11}L + Kc_{10}\gamma_0 > 0. \quad (7.20)$$

The subsystem in R_{uzz}^+ is uniformly persistent whenever

$$\beta_2 = -s_{20} + Kc_{20}\delta_0 > 0. \quad (7.21)$$

Whenever the inequalities (7.20) and (7.21) hold the equilibria in R_{uxy}^+ and R_{uzz}^+ are given by

$$E_6(u_3, x_3, y_3, 0) =$$

$$\left(L + \ell y_3, \frac{K(s_{10}\gamma_0 + \alpha s_{12} - \alpha s_{11}\ell + s_{11}L\gamma_0)}{Kc_{10}\gamma_0^2 - \alpha s_{11}\ell + \alpha s_{12}}, \frac{\alpha\beta_1}{Kc_{10}\gamma_0^2 - \alpha s_{11}\ell + \alpha s_{12}}, 0 \right)$$

and

$$E_7(u_4, x_4, 0, z_4) = \left(L, \frac{s_{20} + s_{22}z_4}{c_{20}\delta_0}, 0, \frac{\alpha\beta_2}{Kc_{20}\delta_0^2 + \alpha s_{22}} \right).$$

The symmetric matrix $\mathcal{B}(u, x, y)$ corresponding to E_6 is given by $b_{11} = \frac{1}{u_3}$, $b_{12} = 0$, $b_{13} = -\frac{\ell u}{2u_3}$, $b_{22} = \frac{\alpha c_{10}}{K}$, $b_{23} = 0$ and $b_{33} = s_{12}$. It is positive definite in the region of attraction whenever

$$s_{12} - \frac{\ell^2}{4u_3}(L + \ell \tilde{M})^2 > 0. \quad (7.22)$$

The matrix corresponding to E_7 , $D(u, x, z) = \text{diag} \left(\frac{1}{u_4}, \frac{ac_{20}}{K}, s_{22} \right)$ is always positive definite.

Thus the system (7.1) will be uniformly persistent whenever inequalities (7.20) - (7.22) hold and

$$\xi = -s_{20} + c_{20}\delta_0 x_3 + c_{30}\xi_0 y_3 > 0, \quad (7.23)$$

and

$$\eta = -s_{10} + s_{11}u_4 + c_{10}\gamma_0 x_4 - \xi_0 z_4 > 0. \quad (7.24)$$

Example 4. When $k = \gamma_1 = \delta_1 = s_{11} = s_{21} = c_{21} = c_{31} = 0$ and $c_{11} > 0$, the mutualist enhances the efficiency of the utilization of the prey by the mutualist-predator. Here the region of attraction is contained in the set

$$B = \{(u, x, y, z) : 0 \leq u \leq L + \ell \tilde{M}, 0 \leq x \leq K, 0 \leq y \leq \tilde{M}, 0 \leq z \leq \tilde{N}\}, \quad (7.25)$$

where

$$\tilde{M} = \frac{-s_{10} + K\gamma_0(c_{10} + c_{11}L)}{s_{12} - K\gamma_0 c_{11}\ell} \quad \text{and} \quad \tilde{N} = \frac{-s_{20} + Kc_{20}\delta_0 + c_{30}\xi_0 \tilde{M}}{s_{22}}.$$

The equilibrium in R_{uz}^+ is $E_3(L, K, 0, 0)$. The subsystems in R_{uzy}^+ and R_{uzy}^+ are uniformly persistent provided

$$\beta_1 = -s_{10} + (c_{10} + c_{11}L)\gamma_0 K > 0, \quad (7.26)$$

and

$$\beta_2 = -s_{20} + Kc_{20}\delta_0 > 0. \quad (7.27)$$

The equilibrium $E_6(u_3, x_3, y_3, 0) = (L + \ell y_3, \frac{K}{\alpha}(\alpha - \gamma_0 y_3), \frac{b + \sqrt{b^2 + 4\alpha\beta_1}}{2Kc_{11}\gamma_0\ell}, 0)$, where

$$b = \alpha(\ell K c_{11} \gamma_0 - s_{12}) - K \gamma_0^2 (c_{10} + c_{11} L).$$

The equilibrium $E_7(u_4, x_4, 0, z_4) = (L, \frac{K(\alpha s_{22} + \delta_0 s_{21})}{\alpha s_{22} + K c_{20} \delta_0^2}, 0, \alpha \beta_2)$.

The symmetric matrix $\beta(u, x, y)$ corresponding to E_6 is given by, $b_{11} = \frac{1}{u_3}$, $b_{12} = 0$, $b_{13} = -\frac{\ell u}{2u_3(L + \ell y)} - \frac{1}{2} c_{11} \gamma_0 x$, $b_{22} = \frac{\alpha}{K}(c_{10} + c_{11} u_3)$, $b_{23} = 0$ and $b_{33} = s_{12}$. It is positive definite in its region of attraction whenever

$$\frac{4s_{12}}{u_3} - \left(\frac{\ell(L + \ell \tilde{M})}{u_3 L} + K c_{11} \gamma_0 \right)^2 > 0. \quad (7.28)$$

The symmetric matrix corresponding to E_7 is given by

$$D(u, x, z) = \text{diag} \left(\frac{1}{L}, \frac{\alpha c_{20}}{K}, s_{22} \right).$$

Thus whenever inequalities (7.26)-(7.28) hold and

$$\xi = -s_{20} - s_{21} u_3 + c_{20} \delta_0 x_3 + c_{30} \xi_0 y_3 > 0, \quad (7.29)$$

and

$$\eta = -s_{10} + (c_{10} + c_{11} u_4) \gamma_0 x_4 - \xi_0 z_4 > 0, \quad (7.30)$$

the given system is uniformly persistent.

Case III We recall from §3.5 that the system (3.1) exhibits obligate mutualism between the mutualist u and the top-predator z whenever the hypotheses $H(1, 2, 3^*, 4^*)$, $G(1, 2, 3')$, $P(1, 2^*)$ and $S(1, 2^*, 3, 4^*)$ hold. Also from hypothesis $S(4^*)$ the mutualism is obligate for the predator. Hence $\mathcal{E}_{z \rightarrow 0}$ in R_{zz}^+ and R_{zyz}^+

and the equilibria E_5 and E_8 do not exist. The criteria for uniform persistence for the subsystems in R_{uxy}^+ and R_{uxz}^+ remain the same as given by Theorem 6.2 and Theorem 6.3, respectively. The following result holds for the system (3.1).

THEOREM 7.5. *Let the hypotheses $H(1, 2, 3^*, 4^*, 5, 10)$, $G(1, 2, 3')$, $P(1, 2^*)$ and $S(1, 2^*, 3, 4^*)$ hold. Then the system (3.1) is uniformly persistent whenever $\xi > 0$ and $\eta > 0$.*

The mutualist u can directly benefit the mutualist-predator z , by enhancing the growth rate of the prey x , by providing an alternate food supply, by increasing its rate of predation or by enhancing the efficiency of utilization of the prey(s). Below we illustrate each of these cases with an example. We also note that the mutualist's interaction with the predator y can also lead to a beneficial effect for the top-predator.

Consider the system

$$\begin{aligned} u' &= u \left(1 - \frac{u}{L + \ell z} \right), \\ x' &= \alpha x \left(1 - \frac{x}{K + ku} \right) - \frac{\gamma_0}{1 + \gamma_1 u} xy - (\delta_0 + 1 + \delta_1 u) xz, \\ y' &= y(-s_{10}) + s_{12} y + \frac{c_1 \gamma_0}{1 + \gamma_1 u} xy - (\xi_0 + \xi_1 u) yz, \\ z' &= z(-s_{20} - s_{21} u - s_{22} z + (c_{20} + c_{21} u)(\delta_0 + \delta_1 u)x + c_3(\xi_0 + \xi_1 u)y), \end{aligned}$$

where all the constants are assumed to be nonnegative.

It is easily seen that in absence of the mutualist $y(t) \leq \frac{-s_{10} + Kc_1\gamma_0}{s_{12}}$. We assume that

$$s_{10} < Kc_1\gamma_0, \quad (7.32)$$

otherwise $\mathcal{E}_{y \rightarrow 0}$ in R_{uzy}^+ . Furthermore for obligate mutualism to occur we require that

$$Kc_{20}\delta_0 + c_3\xi_0 \frac{(-s_{10} + Kc_1\gamma_0)}{s_{12}} \leq s_{20}. \quad (7.33)$$

Example 1 When $\gamma_1 = \delta_1 = \xi_1 = s_{21} = c_{21} = 0$ and $k > 0$, mutualism occurs by means of mutualist enhancing the rate of growth of the prey x .

The region of attraction is contained in the set

$$C = \{(u, x, y, z) : 0 \leq u \leq L + \ell\tilde{N}, 0 \leq x \leq K + k(L + \ell\tilde{N}), 0 \leq y \leq \tilde{M}, 0 \leq z \leq \tilde{N}\}, \quad (7.34)$$

where

$$\tilde{M} = \frac{-s_{10} + c_1\gamma_0(K + k(L + \ell\tilde{N}))}{s_{11}}$$

and

$$\tilde{N} = \frac{-s_{20} + c_{20}\delta_0(K + kL) + c_3\xi_0\tilde{M}}{s_{22} - c_{20}\delta + 0K\ell}.$$

The equilibrium in R_{ux}^+ is $(L, K + kL)$. The subsystems in R_{uzy}^+ and R_{uzy}^+ are uniformly persistent whenever

$$\beta_1 = -s_{10} + c_1\gamma_0(K + kL) > 0, \quad (7.35)$$

and

$$\beta_2 = -s_{20} + c_{20}\delta_0(K + kL) > 0. \quad (7.36)$$

The equilibrium $E_6(u_3, x_3, y_3, 0) = (L, \frac{(K+kL)(\gamma_0 s_{10} + \alpha s_{11})}{\alpha s_{11} + (K+kL)\gamma_0^2 c_1}, \frac{\alpha \beta_1}{\alpha s_{11} + (K+kL)\gamma_0^2 c_1}, 0)$ and $E_7(u_4, x_4, 0, z_4) = (L + \ell z_4, x_4, 0, z_4)$, where $x_4 = \frac{1}{\alpha}(\alpha - \delta_0 z_4)(K + kL + k\ell z_4)$,

$$z_4 = \frac{b_4 + \sqrt{b_0^2 + 4c_{20}\delta_0^2\alpha k\ell\beta_2}}{2c_{20}\delta_0^2 k\ell},$$

and $b_0 = \alpha(-s_{22} + c_{20}\delta_0 k\ell) - c_{20}\delta_0^2(K + kL)$. The symmetric matrix $B(u, x, y)$ corresponding to E_8 is given by $b_{11} = \frac{1}{u_3}$, $b_{12} = \frac{-c_1 \alpha k z}{2(K+ku_3)(K+ku)}$, $b_{13} = 0$, $b_{22} = \frac{\alpha c_1}{K+ku_3}$, $b_{23} = 0$ and $b_{33} = s_{11}$. Thus $B(u, x, y)$ is positive definite in its region of attraction whenever

$$4K^2(K + ku_3) - \alpha u_3 c_1 k^2 (K + kL)^2 > 0. \quad (7.37)$$

The symmetric matrix $D(u, x, z)$ corresponding to E_7 is given by $d_{11} = \frac{1}{u_4}$, $d_{12} = \frac{-\alpha k c_{20} z}{2(K+ku_4)(K+ku)}$, $d_{13} = -\frac{1}{2} \frac{\ell u}{u_4(L+x)}$, $d_{22} = \frac{\alpha c_{20}}{(K+ku_4)}$, $d_{23} = 0$ and $b_{33} = s_{22}$. The region of attraction of the subsystem in $R_{u,x,z}^+$ is contained in the set

$$C_1 = \{(u, x, z) : 0 \leq u \leq L + \ell N_1, 0 \leq x \leq K + k(L + \ell N_1), 0 \leq z \leq N_1\},$$

where $N_1 = \frac{\beta_2}{s_{22} - c_{20}\delta_0 k\ell}$. The matrix $D(u, x, z)$ is positive definite in B_1 whenever

$$4c_{20}s_{22} - \frac{\alpha u_4 c_{20}^2 s_{22} k^2}{(K + ku_4)K^2} (K + kL + k\ell N_1)^2 - \frac{\ell^2}{L^2 u_4} (L + \ell N_1)^2 > 0. \quad (7.38)$$

Thus the system (7.31) is uniformly persistent whenever the inequalities (7.35)-(7.38) hold and

$$\xi = -s_{20} + c_{20}\delta_0 x_3 + c_3 \xi_0 y_3 > 0 \quad (7.39)$$

and

$$\eta = -s_{10} + c_1 \gamma_0 x_4 - \xi_0 z_4 > 0. \quad (7.40)$$

Example 2 When $k = \gamma_1 = \delta_1 = \xi_1 = c_{21} = 0$ and $s_{21} > 0$, mutualism occurs by means of providing an alternate food source to the top-predator. The region of attraction is contained in the set

$$C = \{(u, x, z) : 0 \leq u \leq L + \ell \tilde{N}, 0 \leq x \leq K, 0 \leq y \leq \tilde{M}, 0 \leq z \leq \tilde{N}\}, \quad (7.41)$$

where

$$\tilde{M} = \frac{-s_{10} + Kc_1\gamma_0}{s_{11}} \text{ and } \tilde{N} = \frac{-s_{20} + s_{21}L + Kc_{20}\delta_0 + c_3\xi_0\tilde{M}}{s_{22} - \ell s_{21}}.$$

The equilibrium in R_{uz}^+ is $(L, K, 0, 0)$. The subsystems in R_{uxy}^+ and R_{uzz}^+ are uniformly persistent whenever

$$\beta_1 = -s_{10} + c_1\gamma_0K > 0, \quad (7.42)$$

and

$$\beta_2 = -s_{20} + s_{21}L + c_{20}\delta_0K > 0, \quad (7.43)$$

respectively. In which case the equilibrium

$$E_6(u_3, x_3, y_3, 0) = \left(L, \frac{K(\gamma_0 s_{10} + \alpha s_{12})}{Kc_1\gamma_0^2 + \alpha s_{12}}, \frac{\alpha(-s_{10} + Kc_1\gamma_0)}{Kc_1\gamma_0^2 + \alpha s_{12}}, 0 \right)$$

and

$$E_7(u_5, x_5, 0, z) =$$

$$\left(L + \ell z_4, \frac{K((s_{20} - s_{21}L)\delta_0 + (s_{22} - s_{21}\ell)\alpha)}{Kc_{20}\delta_0^2 + \alpha(s_{22} - s_{21}\ell)}, 0, \frac{\alpha\beta_2}{Kc_{20}\delta_0^2 + \alpha(s_{22} - s_{21}\ell)} \right).$$

The symmetric matrix corresponding to E_6 is $B(u, x, y) = \text{diag}(\frac{1}{u_3}, \frac{\alpha c_1}{K}, s_{12})$.

The symmetric matrix $D(u, x, z)$, corresponding to E_7 is given by $b_{11} = \frac{1}{u_4}$, $b_{12} =$

$0, b_{13} = (\frac{\ell u}{u_4(L+\ell x)} + s_{21}), b_{22} = \frac{\alpha c_{20}}{K}, b_{23} = 0$ and $b_{33} = s_{22}$. The region of attraction of the subsystem in R_{uxz}^+ is contained in the set

$$C_1 = \{(u, x, z) : 0 \leq u \leq L + \frac{\ell \beta_2}{s_{22} - s_{21} \ell}, 0 \leq x \leq K, 0 \leq z \leq \frac{\beta_2}{s_{22} - s_{21} \ell}\}.$$

The matrix $D(u, x, z)$ is positive definite in C_1 whenever

$$s_{22} - u_4(s_{21} + \frac{\ell}{Lu_4}(L + \frac{\ell \beta_2}{s_{22} - s_{21} \ell}))^2 > 0. \quad (7.44)$$

Therefore the system (7.31) will be uniformly persistent whenever inequalities (7.42)-(7.44) hold and

$$\xi = -s_{20} + s_{21} u_3 + c_{20} \delta_0 x_3 + c_3 \xi_0 y_3 > 0, \quad (7.45)$$

and

$$\eta = -s_{10} + c_1 \gamma_0 x_4 - \xi_0 z_4 > 0. \quad (7.46)$$

Example 3 When $k = \gamma_1 = \delta_1 = \xi_1 = s_{21} = 0$ and $c_{21} > 0$, mutualism occurs by mutualist enhancing the utilization of the prey by the top-predator.

Here the region of attraction is contained in

$$C = \{(u, x, y, z) : 0 \leq u \leq L + \ell \tilde{N}, 0 \leq x \leq K, 0 \leq y \leq \tilde{M}, 0 \leq z \leq \tilde{N}\}, \quad (7.47)$$

where

$$\tilde{M} = \frac{-s_{10} + K c_1 \gamma_0}{s_{11}} \text{ and } \tilde{N} = \frac{-s_{20} + (c_{20} + c_{21} L) \delta_0 K + c_3 \xi_0 \tilde{M}}{s_{22} - K c_{21} \ell \delta_0}.$$

The equilibrium in R_{ux}^+ is $E_3(L, K, 0, 0)$. The subsystems in R_{uxy}^+ and R_{uxz}^+ are uniformly persistent whenever

$$\beta_1 = -s_{20} + Kc_1\gamma_0 > 0, \quad (7.48)$$

and

$$\beta_2 = -s_{20} + (c_{20} + c_{21}L)K\delta_0 > 0. \quad (7.49)$$

The equilibrium $E_6(u_3, x_3, y_3, 0)$ in R_{uxy}^+ is the same as in Example 2 and the corresponding matrix $B(u, x, y) = \text{diag}(\frac{1}{u_3}, \frac{\alpha c_1}{K}, s_{12})$. The equilibrium $E_7(u_4, x_4, 0, z_4) = (L + \ell z_4, \frac{s_{20} + s_{22}x_4}{\delta_0(c_{20} + c_{21}u_4)}, 0, \frac{-b_0 + \sqrt{b_0^2 + 4K\ell\alpha\beta_2\delta_0^2c_{21}}}{2\delta_0^2K\ell c_{21}})$, where $b_0 = \alpha s_{22} - K\ell\alpha\delta_0c_{21} + K\delta_0^2(c_{20} + c_{21}L)$. The symmetric matrix $D(u, x, z)$ corresponding to E_7 is given by $d_{11} = \frac{1}{u_4}$, $d_{12} = 0$, $d_{13} = -\frac{1}{2}(\frac{\ell u}{(L + \ell z)u_4} + c_{21}\delta_0 x)$, $d_{22} = \frac{\alpha}{K}(c_{20} + c_{21}u_4)$, $d_{23} = 0$ and $d_{33} = s_{22}$. The region of attraction for the subsystem in R_{uxz}^+ is contained in the set

$$C_1 = \{(u, x, z) : 0 \leq u \leq L + \ell N_1, 0 \leq x \leq K, 0 \leq z \leq \frac{\beta_2}{s_{22} - K\ell\delta_0c_{21}} = N_1\}.$$

The matrix $D(u, x, z)$ is positive definite in A_1 whenever

$$4s_{22} - u_4(\frac{\ell(L + \ell N_1)}{Lu_4} + c_{21}\delta_0 K)^2 > 0. \quad (7.50)$$

Thus if inequalities (7.48)-(7.50) hold and

$$\xi = -s_{20} + (c_{20} + c_{21}u_3)\delta_0 x_3 + c_3\xi_0 y_3 > 0 \quad (7.51)$$

and

$$\eta = -s_{10} + c_1\gamma_0 x_4 - \xi_0 z_4 > 0, \quad (7.52)$$

then the system will be uniformly persistent.

Example 4 When $k = \gamma_1 = \xi_1 = s_{21} = c_{21} = 0$ and $\delta_1 > 0$, mutualism occurs by means of the mutualist increasing the rate of predation by the predator z on the prey x .

$$C = \{(u, x, y, z) : 0 \leq u \leq L + \ell \tilde{N}, 0 \leq x \leq K, 0 \leq y \leq \tilde{M}, 0 \leq z \leq \tilde{N}\} \quad (7.53)$$

where

$$\tilde{M} = \frac{-s_{10} + Kc_1\gamma_0}{s_{11}} \quad \text{and} \quad \tilde{N} = \frac{-s_{20} + c_{20}(\delta_0 + \delta_1 L)K + c_3\xi_0\tilde{M}}{s_{22} - Kc_{20}\ell\delta_1}.$$

The equilibrium in R_{ux}^+ is $E_3(L, K, 0, 0)$. The subsystem in R_{uxy}^+ is uniformly persistent if

$$\beta_1 = -s_{10} + c_1\gamma_0K > 0. \quad (7.54)$$

The equilibrium E_6 in R_{uxy}^+ is the same as in Example 3 and is always globally asymptotically stable with respect to solutions initiating in R_{uxy}^+ .

The subsystem in R_{uxz}^+ will be uniformly persistent whenever

$$\beta_2 = -s_{20} + c_{20}(\delta_0 + \delta_1 L)K > 0. \quad (7.55)$$

The equilibrium in R_{uxz}^+ is $E_7(u_4, x_4, 0, z_4) = (L + \ell z_4, \frac{K}{\alpha}(\alpha - (\delta_0 + \delta_1 u_4)z_4), 0, z_4)$, where z_4 is the unique positive root of the cubic equation

$$k\ell^2 c_{20} \delta_1^2 z^3 + 2K\ell c_{20} \delta_1 (\delta_0 + \delta_1 L)z^2 + (\alpha s_{22} - \alpha K\ell c_{21} \delta_1 + Kc_{20}(\delta_0 + \delta_1 L)^2)z - \alpha\beta_2 = 0.$$

The symmetric matrix $\mathcal{D}(u, x, z)$ corresponding to E_7 is given by $d_{11} = \frac{1}{u_4}$, $d_{12} = \frac{1}{2}c_{20}\delta_1 z$, $d_{13} = -\frac{1}{2}\left(\frac{\ell u}{u_4(L+\ell x)} + c_{20}\delta_1 x\right)$, $d_{22} = \frac{\alpha}{K}c_{20}$, $d_{23} = 0$ and $d_{33} = s_{22}$.

The region of attraction for the subsystem in R_{uxz}^+ is contained in

$$C_1 = \{(u, x, z) : 0 \leq u \leq L + \ell N_1, 0 \leq x \leq K, 0 \leq z \leq \frac{\beta_2}{s_{22} - K\ell c_{20}\delta_1} = N_1\}.$$

The matrix $D(u, x, z)$ is positive definite in A_1 provided

$$s_{22} \left(\frac{4\alpha}{u_4} - Kc_{20}\delta_1^2 N_1 \right) - \alpha \left(\frac{\ell}{u_4 L} (L + \ell N_1) + Kc_{20}\delta_1 \right)^2 > 0. \quad (7.56)$$

Thus whenever the inequalities (7.54)-(7.56) hold and

$$\xi = -s_{20} + c_{20}(\delta_0 + \delta_1 u_3)x_3 + c_3 \xi_0 y_3 > 0, \quad (7.57)$$

and

$$\eta = -s_{10} + c_1 \gamma_0 x_4 - \xi_0 z_4 > 0, \quad (7.58)$$

the given system is uniformly persistent.

7.3 Extinction

Now we consider the situations in which one of the populations in (3.1) or its three-dimensional subsystems becomes extinct.

Case I In case of facultative mutualism between the mutualist u and the mutualist-predator y , the action of the mutualist can result in the extinction of the top-predator. For example, the mutualist could deter the predation of x and/or y by the top-predator z . The proofs of the following two results are same as in §6.3 and are omitted.

Define

$$L_1 = L(\tilde{K}, 0, \tilde{N}), \quad (7.59)$$

where $\tilde{K}$ and $\tilde{N}$ are given by (3.6) then L_1 is a positive lower bound for the eventual mutualist population in (3.1).

THEOREM 7.6. *Let hypotheses $H(1, 2, 3', 4')$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2')$ hold.*

Whenever

$$-s_2(L_1, 0) + c_2(L_1)p_2(L_1, K(L_1)) < 0, \quad (7.60)$$

$\mathcal{E}_{x \rightarrow 0}$ in R_{uzz}^+ .

The extinction criterion for the food chain in R_{zyx}^+ remains the same as given in Theorem 6.9.

THEOREM 7.7. *Let hypotheses $H(1, 2, 3', 4')$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2', 3)$ hold. If*

$$-s_2(L_1, 0) + c_2(L_1)p_2(L_1, K(L_1)) + c_3(L_1)q(L_1, \tilde{M}) < 0, \quad (7.61)$$

where $\tilde{M}$ is given by (3.6), then $\mathcal{E}_{x \rightarrow 0}$ in R_{uzyx}^+ .

Case II In case of obligate mutualism between the mutualist u and the predator y , $\mathcal{E}_{y \rightarrow 0}$ in R_{zyx}^+ . The extinction results given by the above two theorems still remain valid. Further, if the mutualism is ineffective the mutualist-predator y can also become extinct in R_{uzy}^+ and R_{uzyx}^+ .

Define

$$L_2 = L(0, \tilde{M}, 0), \quad (7.62)$$

where $\tilde{M}$ is given by (3.6).

THEOREM 7.8. Let hypotheses $H(1, 2, 3', 4')$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2', 3)$ hold. If

$$-s_1(L_1, 0) + c_1(L_1)p_1(L_1, K(L_2)) < 0, \quad (7.63)$$

$\mathcal{E}_{y \rightarrow 0}$ in R_{uzy}^+ and R_{uzyz}^+ .

THEOREM 7.9. Let hypotheses $H(1, 2, 3', 4')$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2, 3')$ hold if the inequality (7.63) holds and

$$-s_2(L_2, 0) + c_2(L_2)p_2(L_2, K(L_2)) < 0, \quad (7.64)$$

then $\mathcal{E}_{y, x \rightarrow 0}$ in R_{uzyz}^+ .

Case III In case of obligate mutualism between the mutualist and the top-predator, hypothesis $(S4^*)$ implies that $\mathcal{E}_{x \rightarrow 0}$ in R_{zyz}^+ . Below we give extinction criteria for the predator-prey-mutualist subsystems and system (3.1).

Define

$$L^1 = L(\tilde{K}, \tilde{M}, 0) \text{ and } L^2 = L(0, 0, \tilde{N}), \quad (7.65)$$

where $\tilde{K}$, $\tilde{M}$ and $\tilde{N}$ are given by (3.8).

THEOREM 7.10. Let hypotheses $H(1, 2, 3^*, 4^*)$, $G(1, 2, 3')$, $P(1, 2^*)$ and $S(1, 2^*, 3, 4^*)$ hold. If

$$-\tilde{s}_1 + \tilde{c}_1 \tilde{p}_1 < 0, \quad (7.66)$$

where

$$\tilde{s}_1 = \min_{L^1 \leq u \leq L^2} s_1(u, 0), \quad \tilde{c}_1 = \max_{L^1 \leq u \leq L^2} c_1(u) \text{ and } \tilde{p}_1 = \max_{L^1 \leq u \leq L^2} p_1(u, \tilde{K})$$

then $\mathcal{E}_{y \rightarrow 0}$ in R_{uzy}^+ and R_{uzyx}^+ .

THEOREM 7.11. Let hypotheses $H(1, 2, 3^*, 4^*)$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2^*, 3, 4^*)$ hold. If

$$-s_2(L^2, 0) + c_2(L^2)p_2(L^2, K(L^2)) < 0, \quad (7.67)$$

then $\mathcal{E}_{x \rightarrow 0}$ in R_{uwx}^+ .

The above two theorems can be interpreted as follows. If the mutualist has an adverse effect on the predator y then it can eventually become extinct. In case u does not affect the interaction between x and z significantly then $\mathcal{E}_{x \rightarrow 0}$ in R_{uwx}^+ . Further, if the interactions of the food chain are not significantly affected by the presence of the mutualist, the top-predator can become extinct in (3.1).

THEOREM 7.12. Let hypotheses $H(1, 2, 3^*, 4^*)$, $G(1, 2, 3')$, $P(1, 2^*)$ and $S(1, 2^*, 3, 4^*)$ hold. If

$$-s_2(L^2, 0) + c_2(L^2)p_2(L^2, K(L^2)) + c_3(L^2)q(L^2, \tilde{M}) < 0, \quad (7.68)$$

where $\tilde{M}$ is given by (3.8), then $\mathcal{E}_{x \rightarrow 0}$ in R_{uzyx}^+ .

7.4 Reversal of Outcome

In this section we obtain criteria for uniform persistence of (3.1), when in one (or more) of its three-dimensional subsystem(s) a population eventually becomes extinct. In this sense (3.1) can reverse the outcome predicted by its three-dimensional subsystem(s).

Case I

It is clear that if $\mathcal{E}_{y \rightarrow 0}$ in R_{uxy}^+ or in R_{zyz}^+ then $\mathcal{E}_{y \rightarrow 0}$ in R_{uzyz}^+ . However it is possible that due to the action of the mutualist or due to inefficient rate of predation or rate of conversion of prey-biomass to predator biomass, $\mathcal{E}_{x \rightarrow 0}$ in R_{uuz}^+ but (3.1) is uniformly persistent. Specifically we have the following:

THEOREM 7.13. *Let hypotheses $H(1, 2, 3', 4', 5, 6, 9)$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2', 3)$ hold. If the inequality (7.60) holds and $\xi > 0$, then $\mathcal{E}_{x \rightarrow 0}$ in R_{uuz}^+ but (3.1) is uniformly persistent.*

The proof is similar to that of Theorem 6.12. We observe that $\mathcal{E}_{x \rightarrow 0}$ in R_{uuz}^+ , always if the food chain in R_{zyz}^+ is simple.

As an example consider (7.1) with $L = \gamma_0 = 1$, $\ell = \frac{1}{3}$, $\alpha = K = 3$, $k = \gamma_1 = \delta_0 = \delta_1 = c_{11} = c_{21} = c_{31} = 0$, $s_{10} = s_{12} = \frac{1}{3}$, $s_{11} = \frac{1}{24}$, $c_{10} = \frac{1}{4}$, $\xi_0 = \frac{1}{3}$, $s_{20} = s_{22} = \frac{1}{3}$, $s_{21} = 0$, $c_{30} = 2$ and $c_{31} = 0$. The boundary equilibria are $E_0(0, 0, 0, 0)$, $E_1(1, 0, 0, 0)$, $E_2(0, 3, 0, 0)$, $E_3(1, 3, 0, 0)$, $E_4(0, \frac{16}{7}, \frac{5}{7}, 0)$, $E_6(\frac{52}{41}, \frac{90}{41}, \frac{33}{41}, 0)$ and $E_8(0, \frac{12}{5}, \frac{3}{5}, \frac{1}{5})$. The region of attraction is contained in the set

$$B = \{(u, x, y, z) : 0 \leq u \leq \frac{34}{23}, 0 \leq x \leq 3, 0 \leq y \leq \frac{33}{23}, 0 \leq z \leq \frac{43}{23}\}.$$

Since we have a simple food chain, $\mathcal{E}_{x \rightarrow 0}$ in R_{uuz}^+ . Further $\beta_1 = \frac{11}{24}$ and $\gamma = \frac{1}{7}$ imply that the subsystems in R_{uxy}^+ and R_{uzyz}^+ are uniformly persistent.

The symmetric matrix $B(u, x, y)$ corresponding to E_6 is given by $b_{11} = \frac{41}{52}$, $b_{12} = 0$, $b_{13} = -\frac{1}{2}(\frac{41u}{156(1+3y)} + \frac{1}{24})$, $b_{22} = \frac{1}{4}$, $b_{23} = 0$ and $b_{33} = \frac{1}{3}$. The region

of attraction for the subsystem in R_{uxy}^+ is contained in

$$B_1 = \{(u, x, y) : 0 \leq u \leq \frac{34}{23}, 0 \leq x \leq 3, 0 \leq y \leq \frac{33}{23}\}.$$

It is easily seen that $B(u, x, y)$ is positive definite in B_1 .

The symmetric matrix $\mathcal{F}(x, y, z)$ corresponding to E_8 is given by $d_{11} = 1$, $d_{12} = \frac{1}{4}$, $d_{13} = \frac{1}{2}$, $d_{22} = \frac{2}{3}$, $d_{23} = 0$ and $d_{33} = \frac{1}{3}$. Since the matrix $\mathcal{F}(x, y, z)$ is positive definite and $\xi = \frac{25}{123}$, we obtain, (3.1) is uniformly persistent.

Finally we illustrate by an example that it is possible for the food chain in R_{xyz}^+ to be uniformly persistent while, due to the action of the mutualist $\mathcal{E}_{x \rightarrow 0}$ in R_{uxyz}^+ .

Consider the system (7.1) with $L = 1$, $\ell = \frac{1}{3}$, $\alpha = 1$, $k = \gamma_1 = \delta_0 = c_{11} = c_{21} = 0$, $K = 3$, $\gamma_0 = 1$, $s_{10} = s_{12} = \frac{1}{3}$, $s_{11} = s_{21} = 0$, $c_{10} = \frac{1}{4}$, $\xi_0 = 1$, $s_{20} = s_{22} = \frac{1}{4}$, $c_{30} = 1$ and $c_{31} = 5$. Here the mutualist decreases the predator response of the top-predator z .

The boundary equilibria are $E_0(0, 0, 0, 0)$, $E_1(1, 0, 0, 0)$, $E_2(0, 3, 0, 0)$, $E_3(1, 3, 0, 0)$, $E_4(0, \frac{16}{7}, \frac{5}{7}, 0)$, $E_6(\frac{26}{21}, \frac{16}{7}, \frac{5}{7}, 0)$ and $E_8(0, \frac{132}{61}, \frac{17}{61}, \frac{7}{61})$. The region of attraction is contained in the set

$$B = \{(u, x, y, z) : 0 \leq u \leq \frac{17}{12}, 0 \leq x \leq 3, 0 \leq y \leq \frac{5}{4}, 0 \leq z \leq 4\}.$$

Since $\beta_1 = \frac{5}{12}$ and $\gamma = \frac{13}{28}$ the subsystems in R_{uxy}^+ and R_{uxz}^+ are uniformly persistent. But the system (7.1) satisfies the inequality (7.61) and hence $\mathcal{E}_{x \rightarrow 0}$ in R_{uxyz}^+ .

Case II

Under our hypotheses, Theorem 7.4 itself demonstrates reversal of outcome. Further even when $\mathcal{E}_{x \rightarrow 0}$ in R_{uzz}^+ , the system (3.1) can be uniformly persistent.

THEOREM 7.14. *Let hypotheses $H(1, 2, 3', 4', 6)$, $G(1, 2, 3')$, $P(1, 2')$ and $S(1, 2, 3')$ and inequality (7.60) hold. If the equilibrium E_6 is globally asymptotically stable with respect to solutions initiating in R_{uzy}^+ and $\xi > 0$, then the system (3.1) is uniformly persistent, while $\mathcal{E}_{x \rightarrow 0}$ in R_{uzz}^+ .*

The above theorem is always applicable when the food chain in R_{xyz}^+ is simple. Also the action of the mutualist can make the predator-prey-mutualist subsystem in R_{uzz}^+ exhibit extinction. Under our hypotheses this can happen when besides having a beneficial effect on the mutualist-predator (see §7.2, Case II) the mutualist has a detrimental effect on the top-predator, by increasing its death rate or by decreasing its rate of predation or by decreasing the efficiency of utilization of its prey(s). Below we illustrate each of these cases with an example.

Example 1 When $k = \gamma_1 = \delta_1 = s_{11} = c_{21} = c_{31} = 0$, $c_{11} > 0$ and $s_{21} > 0$ for the system (7.1), the mutualist increases the efficiency of utilization of the mutualist-predator and increases the death rate of the top-predator. The region of attraction is contained in the set

$$B = \{(u, x, y, z) : 0 \leq u \leq L + \ell\tilde{M}, 0 \leq x \leq K, 0 \leq y \leq \tilde{M}, 0 \leq z \leq \tilde{N}\}, \quad (7.69)$$

where

$$\tilde{M} = \frac{-s_{10} + K\gamma_0(c_{10} + c_{11}L)}{s_{12} - K\gamma_0 c_{11}\ell} \text{ and } \tilde{N} = \frac{-s_{20} - s_{21}L + Kc_{20}\delta_0 + c_{30}\xi_0\tilde{M}}{s_{22}}.$$

The equilibria in $\overline{R_{ux}^+}$ are $E_0(0, 0, 0, 0)$, $E_1(L, 0, 0, 0)$, $E_2(0, K, 0, 0)$ and $E_3(L, K, 0, 0)$.

The subsystem in R_{uxy}^+ is uniformly persistent whenever

$$\beta_1 = -s_{10} + (c_{10} + c_{11}L)\gamma_0 K > 0. \quad (7.70)$$

Also from Theorem 7.6 the subsystem in R_{uxz}^+ exhibits extinction whenever

$$-s_{20} - s_{21}L + Kc_{20}\delta_0 < 0. \quad (7.71)$$

The equilibrium $E_6(u_3, x_3, y_3, 0) = (L + \ell y_3, \frac{K}{\alpha}(\alpha - \gamma_0 y_3), \frac{b + \sqrt{b^2 + 4\alpha\beta_1}}{2Kc_{11}\gamma_0^2\ell}, 0)$, where $b = \alpha Kc_{11}\gamma_0\ell - \alpha s_{12} - K\gamma_0^2(c_{10} + c_{11}L)$. The matrix corresponding to E_6 is given by $b_{11} = \frac{1}{u_3}$, $b_{12} = 0$, $b_{13} = -\frac{\ell u}{2u_3(L + \ell y)} - \frac{c_{11}\gamma_0 x}{2}$, $b_{22} = \frac{\alpha}{K}(c_{10} + c_{11}u_3)$, $b_{23} = 0$ and $b_{33} = s_{12}$. It is positive definite in its region of attraction if

$$4\frac{s_{12}}{u_3} - \left(\frac{\ell}{u_3 L}(L + \ell\tilde{M}) + Kc_{11}\gamma_0\right)^2 > 0. \quad (7.72)$$

Thus whenever inequalities (7.70)-(7.72) hold and

$$\xi = -s_{20} - s_{21}u_3 + c_{20}\delta_0 x_3 + c_{30}\xi_0 y_3 > 0, \quad (7.73)$$

the system (7.1) is uniformly persistent.

Example 2 When $k = s_{11} = c_{11} = s_{21} = c_{21} = c_{31} = 0$, $\gamma_1 > 0$ and $\delta_1 > 0$ the mutualist enhances the predator response of the mutualist-predator

and decreases that of the top-predator. The region of attraction is contained in the set

$$B = \{(u, x, y, z) : 0 \leq u \leq L + \ell \tilde{M}, 0 \leq x \leq K, 0 \leq y \leq \tilde{M}, 0 \leq z \leq \tilde{N}\}, \quad (7.74)$$

where

$$\tilde{M} = \frac{-s_{10} + Kc_{10}(\gamma_0 + \gamma_1 L)}{s_{12} - Kc_{10}\gamma_1 \ell} \quad \text{and} \quad \tilde{N} = \frac{-s_{20} + Kc_{20}\delta_0/(1 + \delta_1 L) + c_{30}\xi_0 \tilde{M}}{s_{22}}.$$

The equilibria in $\overline{R_{ux}^+}$ are $E_0(0, 0, 0, 0)$, $E_1(L, 0, 0, 0)$, $E_2(0, K, 0, 0)$ and $E_3(L, K, 0, 0)$.

The subsystem in R_{uzy}^+ is uniformly persistent provided

$$\beta_1 = -s_{10} + Kc_{10}(\gamma_0 + \gamma_1 L) > 0, \quad (7.75)$$

in which case the equilibrium $E_6(u_3, x_3, y_3, 0)$ in R_{uzy}^+ is the same as in Example 2 of §7.2 (Case II). Further it is globally asymptotically stable with respect to solutions initiating in R_{uzy}^+ whenever inequality (7.14) holds.

Theorem 7.6 holds whenever

$$-s_{20} + \frac{c_{20}\delta_0}{1 + \delta_1 L} < 0. \quad (7.76)$$

and the subsystem in R_{uxz}^+ exhibits extinction. Thus the system (7.1) is uniformly persistent whenever inequalities (7.14), (7.75), (7.76) hold and

$$\xi = -s_{20} + \frac{c_{20}\delta_0}{1 + \delta_1 u_3} x_3 + c_{30}\xi_0 y_3 > 0. \quad (7.77)$$

Example 3 When $\gamma_1 = \delta_1 = s_{11} = c_{11} = c_{31} = s_{21} = 0$, $k > 0$ and $c_{21} > 0$, the mutualist increases the growth rate of the prey x and decreases the efficiency

of utilization of the prey x by the top-predator. Here the region of attraction is contained in

$$B = \{(u, x, y, z) : 0 \leq u \leq L + \ell \tilde{M}, 0 \leq x \leq K + k(L + \ell \tilde{M}), 0 \leq y \leq \tilde{M}, 0 \leq z \leq \tilde{N}\}, \quad (7.78)$$

where

$$\tilde{M} = \frac{-s_{10} + c_{10}\gamma_0(K + kL)}{s_{12} - c_{10}\gamma_0 k\ell} \text{ and } \tilde{N} = \frac{1}{s_{22}} \left(-s_{20} + \frac{c_{20}\delta_0}{1 + c_{21}L} (K + k(L + \ell \tilde{M})) + c_{30}\xi_0 \tilde{M} \right).$$

The equilibrium in R_{uz}^+ is $E_3(L, K + kL, 0, 0)$ and the subsystem in R_{uzy}^+ is uniformly persistent whenever inequality (7.4) holds. In which case the equilibrium $E_6(u_3, x_3, y_3, 0)$ is the same as in Example 1 (Case III) of §7.2 and is globally asymptotically stable with respect to solutions initiating in R_{uzy}^+ whenever inequality (7.6) holds. The subsystem in R_{uuz}^+ always becomes extinct provided

$$-s_{20} + \frac{c_{20}\delta}{1 + c_{21}L} (K + kL) < 0. \quad (7.79)$$

If in addition

$$\xi = -s_{20} + \frac{c_{20}\delta_0 x_3}{1 + c_{21}u_3} + c_{30}\xi_0 y_3 > 0, \quad (7.80)$$

the system (7.1) will be uniformly persistent.

Finally we note that it is possible for the subsystem in R_{uuz}^+ to be uniformly persistent while the system (3.1) exhibits extinction. To illustrate this we consider Example 1 (Case II) of §7.2, with $L = K = 1$, $k = \frac{1}{4}$, $\ell = s_{10} = s_{12} = s_{20} = s_{22} = c_{10} = \frac{1}{3}$, $\alpha = \delta_0 = 1$, $\gamma_0 = \frac{1}{2}$ and $\xi_0 = c_{20} = c_{30} = 1$. Then the

equilibrium in R_{uz}^+ is $E_3(1, \frac{5}{4})$. Here $\beta_2 = \frac{11}{12}$ implies that the subsystem in R_{uzz}^+ is uniformly persistent. However the mutualist-predator always becomes extinct.

Case III

In the case of obligate mutualism between u and z , Theorem 7.5 itself exhibits reversal of outcome. Further as in previous cases we also have the following result:

THEOREM 7.15. *Let hypotheses $H(1, 2, 3^*, 4^*)$, $G(1, 2, 3')$, $P(1, 2')$, $S(1, 2^*, 3, 4^*)$ and the inequality (7.67) hold. Further let the equilibrium E_6 be globally asymptotically stable with respect to solutions starting in R_{uzyz}^+ and $\xi > 0$. Then $\mathcal{E}_{z \rightarrow 0}$ in R_{uzz}^+ while (3.1) is uniformly persistent.*

Example When $k = \delta_0 = \delta_1 = s_{21} = \xi_0 = 0$, $\gamma_1 > 0$ and $\xi_1 > 0$, the system (7.31) represents interaction of a mutualist with a simple food chain where the mutualist decreases the rate of predation of predator y and the top-predator requires the presence of the mutualist for predation. The region of attraction is contained in the set

$$C = \{(u, x, y, z) : 0 \leq u \leq L + \ell\tilde{N}, 0 \leq x \leq K, 0 \leq y \leq \tilde{M}, 0 \leq z \leq \tilde{N}\}, \quad (7.81)$$

where

$$\tilde{M} = \frac{-s_{10} + \frac{Kc_1\gamma_1}{1+\gamma_1L}}{s_{12}} \quad \text{and} \quad \tilde{N} = \frac{-s_{20} + c_{31}L\tilde{M}}{s_{22} - c_{31}\ell\tilde{M}}.$$

The equilibrium in R_{ux}^+ is $E_3(L, K, 0, 0)$. The subsystem in R_{uxy}^+ will be uniformly persistent whenever

$$\beta_1 = -s_{10} + K \frac{c_1 \gamma_0}{1 + \gamma_1 L} > 0. \quad (7.82)$$

The equilibrium $E_6(u_3, x_3, y_3, 0)$

$= (L, \frac{K(\gamma_0 s_{10} + \alpha(1 + \gamma_1 L)s_{12})(1 + \gamma_1 L)}{\alpha(1 + \gamma_1 L)^2 s_{12} + Kc_1 \gamma_0^2}, \frac{\alpha(Kc_1 \gamma_0 - s_{10}(1 + \gamma_1 L))}{\alpha s_{12}(1 + \gamma_1 L)^2 + Kc_1 \gamma_0^2}, 0)$. The corresponding matrix $B(u, x, y, z)$ is given by $b_{11} = \frac{1}{L}$, $b_{12} = \frac{-c_1 \gamma_0 \gamma_1 y}{2(1 + \gamma_1 L)(1 + \gamma_1 u)}$, $b_{13} = \frac{-c_1 \gamma_0 \gamma_1 z}{(1 + \gamma_1 L)(1 + \gamma_1 u)}$, $b_{22} = \frac{\alpha c_1 \gamma_0^2}{K(1 + \gamma_1 L)^2}$, $b_{23} = 0$ and $b_{33} = s_{12}$. It is positive definite in its region of attraction whenever

$$s_{12} \left(\frac{4\alpha}{KL} - c_1 \gamma_1^2 \tilde{M}^2 \right) + 4\alpha \frac{c_1^2 \gamma_1^2 K}{(1 + \gamma_1 L)^2} > 0. \quad (7.83)$$

— Thus the system will be uniformly persistent whenever inequalities (7.82), (7.83) hold and

$$\xi = -s_{20} + c_3 L \xi_1 y_3 > 0. \quad (7.84)$$

Finally from Theorem 7.11 and Theorem 7.12 we note that whenever $\mathcal{E}_{x \rightarrow 0}$ in R_{uzy}^+ , it does so in R_{uzz}^+ as well.

CHAPTER 8

A MODEL WITH TIME DELAY

8.1 Preliminaries

In this chapter we consider a mutualist-food chain model with a discrete time delay due to gestation, that is, a time delay in conversion of prey biomass to predator biomass. Freedman and Rao (1983) and Erbe et al. (1986) have considered the effects of such a delay in the case of predator-prey systems and for three-species food chains. Here we shall restrict ourselves to the case of facultative mutualism between the mutualist u and the prey x of a simple food chain. Specifically, we consider the model

$$\begin{aligned}u' &= uh(u, x, y) \\x' &= \alpha xg(u, x) - yp(u, x) \\y' &= y[-s_1(u, y) + c_1(u)p(u(t - \tau), x(t - \tau))] - zq(u, y) \\z' &= z[-s_2(u, z) + c_2(u)q(u(t - \tau), y(t - \tau))],\end{aligned}\tag{8.1}$$

with the initial condition $(u(t), x(t), y(t), z(t)) = (u_0(t), x_0(t), y_0(t), z_0(t))$, $t \in [-\tau, 0]$, where $u_0(t)$, $x_0(t)$, $y_0(t)$ and $z_0(t)$ are continuous nonnegative functions on $[-\tau, 0]$.

The parameter τ represents the time delay due to gestation. All the functions in (8.1) are assumed to satisfy the conditions described in §3.2.

The criteria for the existence of various equilibria given in Chapter 4, remain valid for system (8.1). In §8.2 we derive the characteristic equation for

the linear system corresponding to (8.1). In §8.3 we shall consider the effect of delay on the stability of the interior equilibrium E^* and show that increasing the time delay can cause a stable equilibrium to become unstable and cause the population to oscillate. In future work we shall consider the question of boundedness of solutions and that of uniform persistence and extinction for (8.1). In the following we assume that the solutions to the initial value problem (8.1) exist for $t \geq 0$ and are unique.

8.2 The Characteristic Equation

In this section we assume that an interior equilibrium $E^*(u^*, x^*, y^*, z^*)$ exists for the system (8.1). We note that whenever the system (3.1) has an interior equilibrium, so does the system (8.1). To discuss the stability of E^* we consider the linearization of the model (3.1). Let U, V, W and X denote the linearized variables. Then the linear system is given by

$$Y'(t) = AY(t) + BY(t - \tau), \quad (8.2)$$

where

$$Y^T(t) = (U(t), V(t), W(t), X(t)),$$

$$A = \begin{bmatrix} u^* h_u & u^* h_x & u^* h_y & 0 \\ \alpha x g_u - y^* p_u & \alpha g + \alpha x^* g_x - y^* p_x & -p & 0 \\ y^* (-s_{1u} + c'_1 p) - z^* q_u & 0 & -y^* s_{1y} - z^* q_y & -q \\ z^* (-s_{2u} + c'_2 q) & 0 & 0 & -z^* s_{2z} \end{bmatrix},$$

and

$$B = \begin{bmatrix} 0 & & & \\ 0 & 0 & & \\ y^* c_1 p_u & y^* c_1 p_x & 0 & \\ z^* c_2 q_u & 0 & c_2 z^* q_y & 0 \end{bmatrix},$$

where all the functions are evaluated at $E^*(u^*, x^*, y^*, z^*)$.

We seek solutions of the form $\alpha e^{\lambda t}$ of (8.2), where $\alpha \in R^4$. For nontrivial solutions, this leads to the characteristic equation

$$\lambda^4 + a_1 \lambda^3 + a_2 \lambda^2 + a_3 \lambda + a_4 - (\delta_1 \lambda^2 + \delta_2 \lambda + \delta_3) e^{-\tau \lambda} = 0, \quad (8.4)$$

where

$$A = (a_{ij})_{4 \times 4},$$

and

$$a_1 = -\Sigma a_{ii},$$

$$a_2 = (a_{11} + a_{22} + a_{33})a_{44} - a_{13}a_{31} + (a_{11} + a_{22})a_{33} + b_1,$$

$$a_3 = a_{44}(a_{13}a_{31} - (a_{11} + a_{22})a_{33} - b_1) - (a_{31}b_2 + a_{33}b_1) - a_{13}a_{34}a_{41},$$

$$a_4 = a_{44}(a_{31}b_2 + a_{33}b_1) - a_{41}a_{34}b_2,$$

$$\delta_1 = z^*c_2a_{34}q_y + y^*c_1(a_{31}p_u + a_{23}p_z),$$

$$\delta_2 = z^*c_2q_y(a_{41}a_{31} - (a_{11} + a_{22})a_{34}) - y^*c_1(p_u(a_{13}a_{44} - b_2)$$

$$+ p_z(a_{23}a_{44} + b_3)) - z^*c_2q_u a_{13}a_{34},$$

$$\delta_3 = y^*c_1a_{44}(b_3p_z - b_2p_u) + z^*c_2a_{34}(b_1q_y - b_2q_u),$$

$$b_1 = a_{11}a_{22} - a_{12}a_{21}, \quad b_2 = a_{12}a_{23} - a_{13}a_{22},$$

$$b_3 = a_{11}a_{23} - a_{13}a_{21}.$$

8.3 Stability and Hopf bifurcation

The sign of the real parts of the zeros of (8.4) determine the stability of $E^*(u^*, x^*, y^*, z^*)$. Substituting $\lambda = \xi + i\eta$ in (8.4) we obtain

$$\begin{aligned} & \xi^4 - 6\xi^2\eta^2 + \eta^4 + a_1(\xi^3 - 3\xi\eta^2) + a_2(\xi^2 - \eta^2) + a_3\xi + a_4 \\ &= (\delta_1(\xi^2 - \eta^2) + \delta_2\xi + \delta_3)e^{-\tau\xi} \cos \tau\eta \\ &+ (2\delta_1\xi + \delta_2)\eta e^{-\tau\xi} \sin \tau\eta, \end{aligned} \quad (8.5)$$

and

$$\begin{aligned} & 4(\xi^3\eta - \xi\eta^3) + a_1(3\xi^3\eta - \eta^3) + 2a_2\xi\eta + a_3\eta \\ &= (2\delta_1\xi\eta + \delta_2\eta)e^{-\tau\xi} \cos \tau\eta \\ &- (\delta_1(\xi^2 - \eta^2) + \delta_2\xi + \delta_3)\eta e^{-\tau\xi} \sin \tau\eta. \end{aligned}$$

First we consider the case of no stability switching, i.e., derive conditions which ensure that if E^* is stable (unstable) at $\tau = 0$ it would remain stable (unstable) for all $\tau \geq 0$. From the Routh-Hurwitz criterion E^* is stable for $\tau = 0$, whenever

$$A_1 = a_1 > 0, A_2 = a_2 - \delta_1 > 0, A_3 = a_3 - \delta_2 > 0, A_4 = a_4 - \delta_3 > 0,$$

and

$$(A_1 A_2 - A_3) A_3 - A_1^2 A_4 > 0. \quad (8.6)$$

Further E^* will be unstable at $\tau = 0$ if

$$A_1 < 0 \text{ or } A_3 < 0 \text{ or } A_4 < 0. \quad (8.7)$$

Whenever the inequalities (8.6) or (8.7) hold, change in stability can occur only if for some value of τ , the characteristic equation (8.4) has purely imaginary roots. Thus to obtain our stability criterion we set $\xi = 0$ in (8.5) to obtain

$$\eta^4 - a_2\eta^2 + a_4 = (-\delta_1\eta^2 + \delta_3)\cos\tau\eta + \delta_2\eta\sin\tau\eta \quad (8.8a)$$

and

$$-a_1\eta^3 + a_3\eta = \delta_2\eta\cos\tau\eta - (-\delta_1\eta^2 + \delta_3)\sin\tau\eta. \quad (8.8b)$$

Squaring and adding the above two equations, after some simplifications we get

$$\eta^8 + d_1\eta^6 + d_2\eta^4 + d_3\eta^2 + d_4 = 0, \quad (8.9)$$

where

$$\begin{aligned} d_1 &= a_1^2 - 2a_2, \\ d_2 &= a_2^2 + 2a_4 - 2a_1a_3 - \delta_1^2, \\ d_3 &= a_3^2 - 2a_2a_4 + 2\delta_1\delta_3 - \delta_2^2, \end{aligned} \quad (8.10)$$

and

$$d_4 = a_4^2 - \delta_3^2.$$

Noticing that when equations (8.8) have a positive solution then so does equation (8.9), we obtain the following result.

THEOREM 8.1. If the polynomial

$$F(z) = z^4 + d_1 z^3 + d_2 z^2 + d_3 z + d_4 \quad (8.11)$$

has no positive roots then there is no change in stability of E^* for all $\tau \geq 0$.

COROLLARY 8.1. If the inequalities (8.6) hold and $F(z)$ has no positive roots then E^* is locally asymptotically stable for all $\tau \geq 0$.

COROLLARY 8.2. If the condition (8.7) holds then Theorem 8.1 implies that E^* is unstable for all $\tau \geq 0$.

Remark 8.1 From Descartes' rule of signs, Theorem 8.1 holds if $d_i \geq 0$, $i = 1, 2, 3$ and $d_4 > 0$.

THEOREM 8.2. Let the inequalities (8.6) hold. If the polynomial $F(z)$ has at least one positive zero, $z_0 = \eta_0^2$, say, then there exists a τ^* such that E^* is asymptotically stable for $0 \leq \tau < \tau^*$ and unstable for $\tau > \tau^*$, provided

$$\begin{aligned} \alpha(\eta_0) = & \eta_0^2 \{ 4\delta_1^2 e_1 \eta_0^{12} + (3\delta_1^2 e_1 e_2 + 4\delta_1^2 \delta_3^2 - 2\delta_1^2) \eta_0^{10} \\ & + [(2\delta_1^2 e_3 - 1)e_1 + \delta_1^2 (3\delta_3^2 e_2 - 2)e_1] \eta_0^8 \\ & + [\delta_1^2 (\delta_3^2 - 2)e_4 - e_1 e_3] \eta_0^6 \\ & - (e_1 e_4 + 2\delta_1^2 a_4^2) \eta_0^2 - e_1 a_4^2 \} > 0, \end{aligned} \quad (8.12)$$

where

$$e_1 = \delta_2^2 - 2\delta_1\delta_3,$$

$$e_2 = a_1^2 - 2a_2,$$

$$e_3 = a_2^2 + 2a_4 - 2a_1a_3,$$

and

$$e_4 = a_3^2 - 2a_2a_4$$

Further,

$$\tau^* = \min \beta(\eta_0), \quad (8.13)$$

where

$$\beta(\eta_0) = \frac{\delta_2\eta_0(-a_1\eta_0^3 + a_3\eta_0) + (-\delta_1\eta_0^2 + \delta_3)(\eta_0^4 - a_2\eta_0^2 + a_4)}{\delta_2^2\eta_0^2 + (-\delta_1\eta_0^2 + \delta_3)^2}, \quad (8.14)$$

and the minimum is taken over all positive η_0 such that η_0^2 is a zero of the polynomial $F(z)$.

Proof. To establish the existence of τ^* , we first note that η_0 solves the equation (8.9). Now solving equation (8.8a) for $\sin \tau \eta_0$ and substituting in (8.8b) we obtain that for $\tau = \tau_0$ the characteristic polynomial (8.4) has a pair of purely imaginary zeros, $\pm i\eta_0$, where $\tau_0 = \beta(\eta_0)$. Further we notice that if $\pm i\eta_0$ solves the equations (8.8) then η_0^2 solves the equation (8.9). The smallest value of such a τ_0 gives the required τ^* . The theorem will be proved if we can show that $\left. \frac{d\xi}{d\tau} \right|_{\tau=\tau^*} > 0$. Differentiating (8.5) with respect to τ and setting $\xi = 0$, we obtain

$$C(\eta) \frac{d\xi}{d\tau} + D(\eta) \frac{d\eta}{d\tau} = G(\eta),$$

and

$$D(\eta) \frac{d\xi}{d\tau} - C(\eta) \frac{d\eta}{d\tau} = H(\eta), \quad (8.15)$$

where

$$C(\eta) = a_3 - 3a_1\eta^2 + (-\delta_2 + \tau(-\delta_1\eta^2 + \delta_3)) \cos \tau\eta + (\tau\delta_2 - 2\delta_1)\eta \sin \tau\eta,$$

$$D(\eta) = 4\eta^3 - 2a_2\eta + (2\delta_1 - \tau\delta_2)\eta \cos \tau\eta + (-\delta_2 + (-\delta_1\eta^2 + \delta_3)\tau) \sin \tau\eta,$$

$$G(\eta) = \delta_2\eta^2 \cos \tau\eta - (\delta_3 - \delta_1\eta^2)\eta \sin \tau\eta,$$

and

$$H(\eta) = \delta_2\eta^2 \sin \tau\eta + (-\delta_1\eta^2 + \delta_3)\eta \cos \tau\eta.$$

Solving (8.15) with $\tau = \tau^*$, $\eta = \eta_0$ and utilizing (8.8) we get

$$\left. \frac{d\xi}{d\tau} \right|_{\tau=\tau^*} = \frac{\alpha(\eta_0)}{C^2(\eta_0) + D^2(\eta_0)} > 0.$$

Thus for $\tau > \tau^*$ there is at least one zero of (8.4) which has positive real part and E^* is unstable for $\tau > \tau^*$.

THEOREM 8.3. *Let the hypotheses of the Theorem 8.2 hold. If z_0 is a simple zero of the polynomial $F(z)$ and no positive, integer multiple of z_0 is a zero of $F(z)$ then periodic solutions occur as τ crosses τ^* .*

Proof Under the transformation $t = \tau s$ the system (8.2) reduces to a system with fixed delay of size one and its initial conditions are defined by nonnegative, continuous functions on the interval $[-1, 0]$. The result follows as the hypotheses

assumed implies that the conditions of the Hopf-bifurcation theorem (see Hale, 1977) are satisfied. We conclude by illustrating the above results with an example. Consider the system

$$\begin{aligned} u' &= u\left(1 - \frac{1}{L+x}\right), \\ x' &= \alpha x\left(1 - \frac{x}{K}\right) - \gamma_0 xy \\ y' &= y(-s_{10} - s_{11}u - s_{12}y + \frac{c_1}{1+mu}\gamma_0 x - \delta_0 z) \\ z' &= z(-s_{20} - s_{21}u - s_{22}z + c_2\delta_0 y). \end{aligned} \quad (8.16)$$

When $L = 1, K = 5, \alpha = \gamma_0 = 1.5, s_{10} = s_{11} = s_{12} = 0.2, c_1 = 1, m = 0.10, \delta_0 = 1.5, s_{20} = s_{22} = 0.25, s_{21} = 0, c_2 = 0.75$, the system has an interior equilibrium $E^* \approx (2.175, 3.175, .377, .695)$. The coefficients of the characteristic polynomial (8.4) are $a_1 \approx 1.61, a_2 \approx 0.91, a_3 \approx -0.035, a_4 \approx -0.026, \delta_1 \approx -1.84, \delta_2 \approx -1.33$ and $\delta_3 \approx -0.10$. It is easily seen that the inequalities (8.6) hold and therefore E^* is asymptotically stable at $\tau = 0$. The coefficients of the polynomial $F(z)$ are $d_1 \approx 0.77, d_2 \approx -2.51, d_3 \approx -1.34$ and $d_4 \approx -0.01$. Thus from the Descartes' rule of signs $F(z)$ has only one positive zero, which is given by $\eta_0^2 \approx 1.5$. Further $\alpha(\eta_0)$, given by (8.12) is positive and from the formula (8.13), $\tau^* \approx 0.61$. Thus we obtain that E^* is stable for $0 \leq \tau < \tau^*$ and unstable for $\tau > \tau^*$ and that Hopf-bifurcation occurs as τ crosses τ^* .

References

- J.F. Addicott (1984), Mutualistic interactions in population and community processes, in : A New Ecology, Novel Approaches to Interactive Systems (P.W. Price, C.N. Slobodchikoff and B.S. Gaud (editors)), John Wiley, New York.
- J.F. Addicott and H.I. Freedman (1984), On the structure and stability of mutualistic systems: Analysis of predator-prey and competition models as modified by the action of a slow-growing mutualist, Theor. Pop. Biol. 26, 320-339.
- F. Albrecht, H. Gatzke, A. Haddad and N. Wax (1974), The dynamics of two interacting populations, J. Math. Anal. Appl. 46, 658-670.
- A.A. Andronov, L.E. Leontovich, I.I. Gordon and A.G. Maier (1973), Qualitative Theory of Second-order Dynamic Systems, John Wiley, New York.
- N.P. Bhatia and Szegő (1967), Dynamical Systems: Stability Theory and Applications, Springer-Verlag.
- D.N. Boucher (1985), The Biology of Mutualism, Croom Helm, London.
- G. Butler, H.I. Freedman and P. Waltman (1986), Uniformly persistent systems, Proc. Amer. Math. Soc. 96(1986), 425-430.
- G. Butler and P. Waltman (1986), Persistence in dynamical systems, J. Diff. Equations, 63, 255-263.
- K-S Cheng, S-B Hsu and S-S Lin (1981), Some results on global stability of a predator-prey system, J. Math. Biol. 12, 115-126.
- E.A. Coddington and N. Levinson (1955), Theory of Ordinary Differential Equations, McGraw-Hill, New York.
- D.E. Dobbs and R. Hanks (1980), A Modern Course on the Theory of Equations, Polygonal Publ. , New Jersey.
- L.E. El'sgol'ts and S.B. Norkin (1973), Introduction to the Theory and Applications of Differential equations with Deviating Arguments, Academic Press, New York.
- L.H. Erbe, H.I. Freedman and V.S.H. Rao (1986), Three-species food-chain models with mutual interference and time delays Math. Biosci., 80, 57-80.
- H.I. Freedman (1980) Deterministic Mathematical Models in Population Ecology, Marcel Dekker, New York.
- H.I. Freedman, J.F. Addicott and B. Rai (1983), Nonobligate and obligate models of mutualism, in: Population Biology Proceedings (H.I. Freedman and C. Strobeck, editors), Springer Verlag Lecture Notes in Biomathematics, 349-354.
- H.I. Freedman and B. Rai (1987a), Uniform persistence and global stability in models involving mutualism I. Predator-prey-mutualistic systems, in: Mathematical Modelling of Environmental and Ecological Systems (J.B. Shukla, T.G. Hallam, V. Capasso, editors), Elsevier Science Publishers, Amsterdam

- H.I. Freedman, J.F. Addicott, B. Rai (1987b), Obligate mutualism with a predator: stability and persistence of three-species models, J. Theor. Biol. 32, 157-175.
- H.I. Freedman and B. Rai (1987c), Persistence in a predator-prey-competitor-mutualist model, in: Proceedings of the Eleventh International Conference on Nonlinear Oscillations (M. Farkas, V. Kertesz and G. Stepan eds), Janos Bolyai Math. Soc., Budapest, 73-79.
- H.I. Freedman and B. Rai (1987d), Uniform persistence and global stability in models involving mutualism 2. Competitor-Competitor-mutualist system, Indian Jour. Math. (to appear).
- H.I. Freedman and V.S. H. Rao (1983), The trade-off between mutual interference and time lags in predator-prey systems, Bull. Math. Biol. 45, 991-1004.
- H.I. Freedman and J.W.-H. So (1985), Global stability and persistence of simple food chains, Math. Biosci. 76, 69-86.
- H.I. Freedman and P. Waltman (1977), Mathematical analysis of some three-species food-chain models, Math. Biosci. 33, 257-276.
- H.I. Freedman and P. Waltman (1984), Persistence in models of three interacting predator-prey populations, Math. Biosci. 68, 213-231.
- H.I. Freedman and P. Waltman (1985), Persistence in a model of three competitive populations, Math. Biosci. 73, 89-101.
- F.R. Gantmacher (1959), The Theory of Matrices (volume 2), Chelsea Publishing Company, New York.
- B.S. Goh (1980), Management and Analysis of Biological Populations, Elsevier Scientific Publ. Co., New York.
- K.P. Hadeler and D. Glas (1983), Quasimonotone systems and convergence to equilibrium in a population genetic model, J. Math. Anal. Appl. 95, 297-303.
- J.K. Hale (1969), Ordinary Differential Equations, Wiley-Interscience, New York.
- J. Hale (1977), Theory of Functional Differential Equations, Springer-Verlag, Heidelberg.
- P. Hartman (1982), Ordinary Differential Equations, Birkhäuser, Boston.
- B.D. Hassard, N.D. Kazarinoff and Y.-H. Wan (1981), Theory and Applications of Hopf Bifurcation, Cambridge University Press, Cambridge.
- M.W. Hirsch (1982), Systems of differential equations which are competitive or cooperative. I: Limits Sets, SIAM J. Math. Anal. 13, 167-179.
- M.W. Hirsch (1985), Systems of differential equations that are competitive or cooperative II: Convergence almost everywhere, SIAM J. Math. Anal. 16, 423-439.

- S.B. Hsu (1978), On global stability of a predator-prey system, Math. Biosci. 39, 1-10.
- A.N. Kolmogorov (1936), Sulla teoria di Volterra della lotta per l'esistenza, Gior. Istituto Ital. Attuari. 7, 74-80.
- L-P Liou and K-S Cheng (1988), Global stability of a predator-prey system, J. Math. Biol. 26, 65-71.
- J.C. Nickerson, C.A. Rolph Kay, L.L. Buschman and W.H. Whitcomb (1977), The presence of *Spissistilus festinus* as a factor affecting egg predation by ants in soybeans, Flor. Ent. 60, 193-199.
- L.G. Monteith (1960), Influence of plants other than the food plants of their host on host-finding by tachinid parasites, Can. Ent. 92, 641-652.
- V.V. Nemytskii and V.V. Stepanov (1960), Qualitative Theory of Differential Equations, Princeton University Press, Princeton.
- S.L. Pimm and J.H. Lawton (1978), On feeding on more than one trophic level, Nature 275, 542-544.
- P.W. Price, C.E. Bouton, P. Gross, B.A. McPherson, J.N. Thompson, and A.E. Weis (1980), Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies, Ann. Rev. Ecol. Syst. 11, 41-65.
- B. Rai, H.I. Freedman and J.F. Addicott (1983), Analysis of three species models of mutualism in predator-prey and competitive systems, Math. Biosci. 65, 13-50.
- B. Rai and S.K. Rai (1988), A simple food chain: Interaction with a mutualist (preprint).
- A. Rescigno (1967), The struggle for life. I: two species, Bull. Math. Biophys. 29, 377-388.
- H.L. Smith (1986a), On the asymptotic behaviour of a class of deterministic models of cooperating species, SIAM J. Appl. Math. 46, 368-375.
- H.L. Smith (1986b), Periodic solutions of periodic competitive and cooperative systems, SIAM J. Math. Anal. 17, 1289-1318.
- H.L. Smith (1986c), Cooperative systems of differential equations with concave nonlinearities, Nonlinear Anal. TMA 10, 1037-1052.
- H.L. Smith (1986d), Competing subcommunities of mutualists and a generalized Kamke Theorem, SIAM J. Appl. Math. 46, 856-874.
- Y. Takeuchi, N. Adachi and H. Tokumaru (1978), Global stability of ecosystems of the generalized Volterra type, Math. Biosci. 42, 119-136.
- Y. Takeuchi and N. Adachi (1980), The existence of globally stable equilibria of ecosystems of the generalized Volterra type, J. Mathematical Biology 10, 401-415.

C.L. Wolin (1985), The population dynamics of mutualistic systems, in: The Biology of Mutualism (D.H. Boucher, editor), 248-269 Croom Helm, London.

G.N. Wolcott (1942), The requirements of parasites for more than hosts, Science 96, 317-318.

S. Zheng (1986), A reaction-diffusion system of a predator-prey-mutualist model, Math. Biosci. 78, 217-245.